ISSN 0753-4973

ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

March 2009

Volume 26, N° 1-4

ISSCA
International Society for the Study and Conservation of Amphibians
(International Society of Batrachology)

SEAT

Reptiles et Amphibiens, Département de Systématique et Evolution, Muséum national d'Histoire naturelle, CP 30, 25 rue Cuvier, 75005 Paris, France. – Tel.: (33).(0)1.40.79.34.87. – Fax: (33).(0)1.40.79.34.88. – E-mail: ohler@mnhn.fr.

BOARD FOR 2008

President: Jon LOMAN (Lund, Sweden).
General Secretary: Annemarie OHLER (Paris, France).
Treasurer: Stéphane GROSJEAN (Paris, France).
Councillors: Lauren E. BROWN (Normal, USA); Rafael O. DE SÁ (Richmond, USA); Rémi DUGUET (Saint-André, France); JIANG Jianping (Chengdu, China); Esteban O. LAVILLA (San Miguel de Tucumán, Argentina); Edgar LEHR (Lawrence, USA); Thierry LODE (Angers, France); Stefan LÖTTERS (Amsterdam, The Netherlands); Alain PAGANO (Angers, France); Heike PRÖHL (Hannover, Germany) ; Miguel VENCES (Braunschweig, Germany).

TARIFF FOR 2008

TARIFF FOR INDIVIDUALS

Regular 2008 subscription to *Alytes* (volume **26**) + ISSCA + *Circalytes*	50 € or 75 $
Student 2008 subscription to *Alytes* (volume **26**) + ISSCA + *Circalytes*	25 € or 37.50 $
SPECIAL OFFER: gift half-price subscription of one year for a colleague of your choice:	**Half of price above**
Regular 2008 subscription to *Alytes* (volume **26**) alone	46 € or 69 $
Student 2008 subscription to *Alytes* (volume **26**) alone	23 € or 34.50 $
Back issues of *Alytes*: any single issue	15 € or 22.50 $
Back issues of *Alytes*: any double issue	25 € or 37.50 $
Back issues of *Alytes*: any complete volume (4 issues)	40 € or 60 $
Back issues of *Alytes*: complete set of volumes **1** to **25** (1982-2007)	720 € or 1125 $
Regular five-year (2008-2012, volumes **26** to **30**) individual subscription to *Alytes* + ISSCA + *Circalytes*	225 € or 337.50 $
Regular five-year (2008-2012, volumes **26** to **30**) individual subscription to *Alytes*	200 € or 300 $
SPECIAL OFFER: five-year (2008-2012, volumes **26** to **30**) individual subscription to *Alytes* + ISSCA + *Circalytes*, with complete set of back issues of *Alytes* (1982-2007, volumes **1** to **25**)	825 € or 1237.50 $
Life individual subscription to *Alytes* from 2008 on	1080 € or 1620 $
Life individual subscription to *Alytes* + ISSCA + *Circalytes* from 2008 on	1200 € or 1800 $
Patron individual subscription to *Alytes* from 2008 on	2160 € or 3250 $ **or more**
Patron individual subscription to *Alytes* + ISSCA + *Circalytes* from 2008 on	2400 € or 3600 $ **or more**

	Take away	Mailing Europe	Mailing outside Europe
Monalytes (volume **1** or volume **2**) 2008	40 € or 60 $	60 €	97.50 $
Monalytes (volume **1** and **2**) 2008	70 € or 105 $	110 €	180 $

TARIFF FOR INSTITUTIONS

2008 subscription to *Alytes* (volume **26**) + ISSCA + *Circalytes*	100 € or 150 $
2008 subscription to *Alytes* (volume **26**) alone	92 € or 138 $
Back issues of *Alytes*: any single issue	30 € or 45 $
Back issues of *Alytes*: any double issue	50 € or 75 $
Back issues of *Alytes*: any complete volume (4 issues)	80 € or 120 $
Back issues of *Alytes*: complete set of volumes **1** to **25**	1500 € or 2250 $
SPECIAL OFFER: five-year (2008-2012, volumes **26** to **30**) institution subscription to *Alytes* + ISSCA + *Circalytes*, with complete set of back issues of *Alytes* (1982-2007, volumes **1** to **25**)	1650 € or 2475 $

	Take away	Mailing Europe	Mailing outside Europe
Monalytes (volume **1** or volume **2**) 2008	80 € or 120 $	100 €	157.50 $
Monalytes (volume **1** and **2**) 2008	140 € or 210 $	180 €	285 $

MODES OF PAYMENT

– In Euros, by cheques **drawn on a French bank** payable to "ISSCA", sent to our secretariat (address above).

– In Euros, by direct postal transfer to our postal account: "ISSCA", Nr. 1-398-91 L, Paris. **If you use this mode of payment, add 2.50 € to your payment for postal charges at our end.**

– In US Dollars, by credit card or by cheque sent to: Bibliomania!, P.O. Box 58355, Salt Lake City, UT 84158, USA: phone/fax: +1-801-562-2660; e-mail: breck@herplit.com.

ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

March 2009 **Volume 26, N° 1-4**

Alytes, 2009, **26** (1-4): 1-85.

A new ergotaxonomy of the family Salamandridae Goldfuss, 1820 (Amphibia, Urodela)

Alain DUBOIS* & Jean RAFFAËLLI**

* Reptiles & Amphibiens, UMR 5202 CNRS OSEB,
Département Systématique & Évolution, Muséum national d'Histoire naturelle,
CP 30, 25 rue Cuvier, 75005 Paris, France
<adubois@mnhn.fr>

** Penclen, 56420 Plumelec, France
<jean.raffaelli@laposte.net>

Several recent studies, particularly dealing with molecular phylogeny, have improved our knowledge of the relationships within the salamander family SALAMANDRIDAE. However, some only of these findings have resulted in formal taxonomic changes. In order to homogenize this taxonomy, we hereby recognize several new taxa at various ranks from subfamily to subspecies, and we propose a new comprehensive ergotaxonomy and nomenclature for the whole family. We also discuss some general questions of taxonomy and nomenclature, in particular regarding the concepts of species and genus, the use of taxonomic categories and nomenclatural ranks in taxonomy, the relationships between taxonomy and conservation biology, the various modes of definition of taxa (including diagnoses and cladognoses), the structure and length of scientific nomina, the status of online databases providing taxonomic and nomenclatural data, the designation of nucleospecies of nominal genera and the nomenclatural status of various nomina.

CONTENTS

Abstract 1
Terminological note 2
Introduction 3
Taxonomic methods and concepts 5
    Taxonomy and nomenclature 5
    Eidonomy: specific and infraspecific classification 6

- Phylonomy: supraspecific classification........ 8
  - Nomenclatural ranks........ 10
  - The use of hybridization data in taxonomy........ 13
  - Taxognoses........ 15
- Comments on nomenclature........ 17
  - Zoological nomina should be short and simple........ 17
  - Nucleospecies designations for genera........ 22
  - The nomenclatural status of websites dealing with AMPHIBIA........ 23
  - The nomina created by DE LA CEPÈDE (1788*a-b*)........ 26
  - The nomenclatural status of the urodelan generic nomina created by RAFINESQUE (1815)........ 27
- Proposed taxonomic changes in the family *SALAMANDRIDAE*........ 29
  - Subfamilies........ 29
  - Tribes, subtribes and infratribes........ 29
  - Genera and subgenera........ 31
  - Supraspecies, species, exerges and subspecies........ 34
- New, resurrected and emended taxa, nucleospecies designations and nomenclatural comments........ 40
- Conclusion........ 67
- Acknowledgements........ 69
- Literature cited........ 69

> "The whole of the Salamandridae require a thorough examination, in order that the relations of the different groups may be properly appreciated, and their characters fully established."
>
> BELL, 1839: 134

> "Ideally, all species that exist in each group should be recognized taxonomically. If biologists fail to detect undescribed species revealed by their studies, they are making one kind of error, and if they recognize more species than exist in nature, they are making a second kind of error."
>
> HIGHTON, 2000: 215

> "No names, no conservation."
>
> PARRA et al., 2005: 45

TERMINOLOGICAL NOTE

In the present work, we strictly respect the rules of the *International Code of Zoological Nomenclature* (ANONYMOUS, 1999; "the *Code*" below), but we sometimes use different terminologies to designate the concepts of the *Code*, for reasons explained in detail by DUBOIS (2000, 2005*b*). We use the term *nomen* (plural *nomina*) for "scientific name" and the term *nominal-series* for the three "groups of names" recognized by the *Code*: *family*-, *genus*- and *species-series*. The use of the term "type" in nomenclature may be misleading (DUBOIS, 2005*b*), and this term is appropriately replaced by the term *onomatophore* (SIMPSON, 1940). There are different kinds of onomatophores. Those of family-series and genus-series nomina, termed respectively "type-genus" and "type-species" in the *Code*, are nominal taxa respectively of rank genus and species. They are designated below respectively by the terms *nucleogenus* and *nucleospecies* (DUBOIS, 2005*a-b*), which are not based on the root "type". Onomatophores of species-series nomina are *onymophoronts*, that can be designated as *holophoronts*, *symphoronts*, *lectophoronts* and *neophoronts* (for "holotypes", "syntypes", "lectotypes" and "neotypes"). For the same reason, the term *monophory* (DUBOIS, 2005*b*) is here used instead of "monotypy" as used in the *Code*, and the term *onymotope* (DUBOIS, 2005*b*) instead of "type locality". The term *neonym* (DUBOIS, 2000) is here used to designate the concept called "new replacement name", "nomen substitutum" or "nomen novum" in various successive editions of the *Code*, and the term *archaeonym* (DUBOIS, 2005*b*) to designate the nomen replaced by a neonym. The term *anoplonym* (DUBOIS, 2000) designates a nomen that is not nomenclaturally available according to the *Code*; a frequently used subcategory of anoplonym is that of *gymnonym* (DUBOIS, 2000), a concept called "nomen nudum" in the *Code*. A distinction is made below between the formula *new combination*, in the strict sense of the *Code*, which involves a change in generic nomen, and the more general formula *new onymorph* (SMITH & PEREZ-HIGAREDA, 1986), which designates any different association of terms, with or without change in generic nomen, in a binomen or trinomen (see DUBOIS, 2000). Finally, DUBOIS (2006*b*) proposed to replace the *Code*'s term "nominotypical" by the term *hyponymous*: among two taxa hierarchically related and referred to the same series that bear the same nomen because of the Principle of Coordination, the term *epinym* designates the nomen of the superordinate taxon, and *hyponym* that of the subordinate taxon, both terms being *eponyms*. New nomenclatural acts implemented in this study or identified for the first time in previous works are pointed out below in bold characters: e.g., **new combination**, **new synonym**, **valid nucleospecies designation**.

INTRODUCTION

Taxonomy is a scientific discipline in permanent evolution, and will remain so for a long time still. This is mostly due to the importance of the *taxonomic impediment* (ANONYMOUS, 1994): only a small fraction of the earth's biodiversity has already been collected and studied, and many pieces of information (on morphology, behaviour, genetics, phylogeny, distribution) about most "known" (i.e., named) taxa are still missing. For this reason, the classification of living organisms cannot be stable, and pleas for "taxonomic stability" amount in fact to apologies of ignorance (GAFFNEY, 1977, 1979; DOMINGUEZ & WHEELER 1997; DUBOIS, 1998*a*).

This is particularly true of the class **AMPHIBIA**, for which we are still far from having a complete or "subcomplete" list of the species still inhabiting our planet, many of which are threatened with extinction (STUART et al., 2008). The recent years have witnessed an unprecedented burst of works (1) describing new species and (2) proposing new hypotheses for the cladistic relationships between the known species, resulting in the recognition of new supraspecific taxa. It is likely that this trend will continue for several decades, and we are clearly in a very exciting period of the history of amphibian taxonomy.

The recent "*boost in species discoveries in a highly endangered vertebrate group*" (KÖHLER et al., 2005) has another important consequence. Strategies in global conservation policy devised on the basis of a highly incomplete or misleading taxonomy may prove inadequate, inefficient or even counter-productive (DUBOIS, 2003*a*). As pointed out by PARRA et al. (2005), development of a good taxonomy is a major requirement for the proper establishment of conservation priorities. This requires an intensification of field and laboratory work to collect and identify unknown species and for ascertaining species limits, recognition of so-called "cryptic" species or *dualspecies* (BERNARDI, 1980), and proper appraisal of *biodiversity hotspots* (see e.g. MEEGASKUMBURA et al., 2002) and of unique, isolated holophyletic groups, without close relatives in today's fauna. These data are crucial for establishing taxonomic and geographic priorities in conservation strategies.

An important aspect of this question is that conservation actions are often facilitated, not to say made possible, by the existence of a *taxonomic and nomenclatural recognition* of the units to be protected (species, subspecies): most legislative texts, red lists, custom documents, etc., only recognize such units if these bear Latin taxonomic nomina. The statement "*No names, no conservation*" (PARRA et al., 2005: 45) is warranted not only because identification of species (and other lower taxa) is necessary for proper appreciation of the conservation priorities, but also because it is often impossible to call for the legal protection of a "population" if it is unnamed taxonomically. This problem was well illustrated by a recent paper of MONTORI et al. (2008) about *Calotriton asper*, where the authors stated that, given the difficulties encountered for recognizing and naming taxa in this group, "*according to general conservation practices, none of the extremely differentiated populations of* C. asper *would be included in specific conservation plans*", although "*loosing any differentiated population would imply the loss of the evolutionary process leading to that particular morphology*" (p. 48).

This is true not only at specific or infraspecific level, but also in higher taxonomy. It is important to recognize taxonomically holophyletic groups at various levels above species, even if they include a single or few species, or even perhaps more for this reason: thus, in salamanders, knowing that the genera *Protohynobius*, *Dicamptodon* or *Hemidactylium* are the unique genera of their subfamilies or families currently alive (RAFFAËLLI, 2007) should call special attention of conservation biologists to these organisms.

Thus, to be fully efficient in conservation biology, any evolutionary, phylogenetic or taxonomic analysis of a population or group of populations that points to its uniqueness or distinctness must go to its end, i.e., to the formal taxonomic and nomenclatural recognition of this unit. Phylogenetic or other analyses uncovering new taxa that are not followed by their taxonomic recognition and naming amount to what BOCQUET (1976: 319) has called "taxonomic cramps", which are in fact scientific errors, as highlighted by HIGHTON (2000, liminar citation above).

An additional, purely nomenclatural, problem is posed by the fact that, at low taxonomic levels, the nomenclatural transcription of trees of hypothesized relationships is made difficult by the arbitrary limitations imposed by the *Code* to the number of ranks that can be used in zoological nomenclature. Thus, in the genus-series of nomina, the *Code* only allows the recognition of two ranks, genus and subgenus. With the quick increase in the number of taxa that recent cladistic analyses often lead to recognize, this is clearly insufficient, and this explains the temptation of some to create additional ranks, not recognized by the *Code*, such as supergenus (e.g., RAFFAËLLI, 2007; VIEITES et al., 2007) or series of successive ranks below subgenus and above species (e.g., HILLIS et al., 2001; HILLIS & WILCOX, 2005). Similarly, below the rank species, the *Code* only allows the use of two ranks, subspecies and "aggregate of subspecies". It is clear that more ranks would be really necessary in zootaxonomy (DUBOIS, 2006*a-c*, 2007*c*), especially to express taxonomically fine cladistic relationships between species and phylogeographic relationships among populations of a species, and for use in conservation biology. However, until the *Code* is modified to allow for their recognition, the use of such ranks is not *Code*-compliant and should not be encouraged.

In the recent years, within the class AMPHIBIA De Blainville, 1816, some groups of the order URODELA Duméril 1806, and particularly in the family *PLETHODONTIDAE* Gray, 1850, have experienced important revisionary works and descriptions of new taxa (DUBOIS, 2005*c*; RAFFAËLLI, 2007). The family *SALAMANDRIDAE* Goldfuss, 1820 has been only moderately concerned by these changes. Several recently published studies, as well as our own experience of these animals, suggest that the whole taxonomy of this family should be revised. In particular, the cladistic relationships hypothesized by WAKE & ÖZETI (1969) on the basis of morphological characters, that have been considered valid for several decades, were only partially confirmed by molecular data. A few changes have already been brought to this taxonomy recently, but they were partial, dealing only with some genera or groups of genera and leaving other taxa unmodified. This results in an unbalanced taxonomy which reflects only partially the recent increase in our knowledge of these salamanders. Our aim below is to propose a new *ergotaxonomy* (DUBOIS, 2005*b*) incorporating these new findings. This is certainly not the last word on this question, as the foreseeable discovery of new species, the re-evaluation of the status of some of the known species, and new cladistic data, based on both molecular and morphological analyses, will certainly be followed by other changes.

Finally, another important motivation for our proposals, similar to that of DUBOIS (1992) in the anuran family *RANIDAE*, is purely nomenclatural. It is to propose short and simple nomina for some taxa which will no doubt have to be recognized, sooner or later, by some authors in the future, and thus to avoid the publication for them of uselessly long, awkward and unpalatable nomina, which could not be modified by subsequent authors. Although this question is rarely tackled in scientific publications, we offer below a few general comments on the principles that should, in our opinion, guide the etymology, aspect, structure and length of zoological nomina.

TAXONOMIC METHODS AND CONCEPTS

TAXONOMY AND NOMENCLATURE

Although confused by some, taxonomy and nomenclature are two distinct fields. Taxonomy provides a classification of organisms into *taxa*, whereas nomenclature provides *nomina* to designate these taxa but does not deal with their establishment or definition. The existence of a universal nomenclature of living taxa regulated by international rules is a major social need as we need non-ambiguous designations for the same objects in all domains of activities, e.g., scientific publications, juridical texts, trade and custom documents, conservation biology, etc. This strong constraint implies that all these texts and documents follow the same nomenclatural system with a single nomenclatural hierarchy of taxa, in particular using similar binominal Latin nomina for "species". This does not mean that all taxa referred to this rank should be "equivalent" by some criterion: as a matter of fact, several different "kinds of species" need to be recognized in different situations. This has long been misunderstood, because of the frequent confusion made between the taxonomic concept of *taxonomic category* and the nomenclatural tool of *nomenclatural rank* (for more details, see DUBOIS, 2007*a*, 2008*d*). Here we make the distinction between these two concepts, which implies in particular that different taxonomic categories can be referred to the same nomenclatural rank.

Taxonomy consists in two rather different subfields that use largely different methods and concepts. The first one, the "science of species", was called *microtaxonomy* by MAYR & ASHLOCK (1980) and *eidonomy* by DUBOIS (2008*b*,*d*). Its duty is to define, recognize and describe taxa of nomenclatural rank *species*. These taxa can be hierarchically arranged in more comprehensive taxa of higher ranks, and nowadays all authors agree that this arrangement should reflect somehow the phylogenetic relationships between organisms. This is the role of the second subfield of taxonomy, called *macrotaxonomy* by MAYR & ASHLOCK (1991) but that could better be designated as *phylonomy* (from the Greek *phulon*, in the sense of "kind, class", and *-nomos*, derived from *nemo*, in the sense of "I divide, I distribute"). This latter term is of more general meaning that that of *cladonomy* (BRUMMITT, 1997; DUBOIS, 1997, 2007*a*), which designates a particular conception of phylonomy that takes into account only the cladistic relationships between taxa, without caring for their age or their degree of divergence, a conception which is not shared by all taxonomists. This terminological difference is rooted in a traditional one in the literature on biological evolution that has been ignored in the recent years (MAYR & ASHLOCK, 1991: 206), the term *phylogenesis* (or phylogeny) being considered to apply to a combination of *cladogenesis* and *anagenesis* (sensu HUXLEY, 1957) (or *cladogeny* and *anageny*), whereas in many recent publications the terms *phylogeny* and cladogeny are considered synonyms, and the term anageny (and the concept to which is refers) ignored altogether.

We present below briefly the guidelines that we have followed here in our eidonomic and phylonomic decisions.

EIDONOMY: SPECIFIC AND INFRASPECIFIC CLASSIFICATION

Many theoretical discussions and publications have dealt with the "species concept". As discussed elsewhere in detail (DUBOIS, 2008*b*, 2009*b*), many of these discussions were obscured by the confusion made between different meanings of the term "species", in particular between its taxonomic and nomenclatural meanings. As a nomenclatural tool, *species* is a universal device allowing the allocation of any individual to a taxon of this rank, whatever philosophy of taxonomy is followed and whatever biological characteristics allow to define or recognize this taxon. In contrast, different taxonomic concepts of "species" have been and are used by taxonomists of different "schools" or to accommodate natural entities having widely different characteristics. These several distinct *taxonomic categories* or "specion" concepts, such as *mayron*, *simpson*, *klepton* or *klonon*, can be used for taxa at the *nomenclatural rank* species (DUBOIS, 1991, 2007*a*, 2008*b*,*d*, 2009*b*).

We here adopt a practical viewpoint that should in our opinion be used in salamandrids, as well as in most other zoological groups (DUBOIS, 2008*b*, 2009*b*). There exists a wide variety of evolutionary situations in nature, and, above all, a wide variety of information available to taxonomists. Requiring to apply a single, "unified", taxonomic species concept to all situations is possible only through using the "smallest common denominator" to all cases, i.e., through losing a lot of information which is sometimes available (and then useful), but sometimes not. This would be similar to taking advantage, for establishing the phylogeny and taxonomy of all vertebrates, only of the information available both for all fossil and recent known species, i.e., derived from the study of their skeleton. In contrast and in practice, to build their classifications, vertebrate taxonomists make use of all available characters, which are not as numerous and as varied in all cases.

Regarding the taxonomic species concept, the clearest situation is that of two entities occurring synchronically, sympatrically or parapatrically, and accessible to morphological, genetic, molecular, karyological, behavioural and other studies. Such studies can allow to know whether a free bi-directional gene flow exists between the two entities, or whether this gene flow is absent, or restricted, unbalanced or uni-directional: whatever the reasons for this restriction in gene flow, such entities must be treated as species under a "biological" or "mixiological" taxonomic species concept (MAYR, 1942, 1963) or *mayron* (DUBOIS, 2007*a*), whereas entities connected by a free symmetrical gene flow must be considered conspecific, although possibly as different taxonomic subspecies. However, whenever two entities are allochronic or allopatric, or are not accessible to the studies mentioned above, this concept cannot be used and it is necessary to have recourse to "inference", through comparison with other "similar" pairs of entities, using for example "genetic distances", although the latter by themselves do not provide unambiguous information on the existence or potentiality of gene flow between two entities (DUBOIS, 1977, 1998*a*). In such cases, we are bound to use an "evolutionary" or "phylogenetic" taxonomic species concept or *simpson* (DUBOIS, 2007*a*), just like in paleontology we are bound to use only skeletal data for phylogenetic analysis and taxonomic decisions in the absence of other information. We used these concepts in our specific and subspecific taxonomy of the *SALAMANDRIDAE*. From a practical viewpoint, in several cases we tend to agree with HIGHTON (2000) in recognizing more species than in more traditional taxonomies.

In several amphibian groups, particular kinds of taxonomic species exist, for which the taxonomic categories of *zygoklepton* and *gynoklepton* can be used (DUBOIS, 1977, 1991, 2008*b*, 2009*b*; DUBOIS & GÜNTHER, 1982), but so far such kinds of entities have not been described in the *SALAMANDRIDAE*. In contrast, in this well-studied family, many taxa need to be recognized at ranks below species, not only for "pure" taxonomic reasons but sometimes for "practical" reasons related to conservation issues.

The recent development of the discipline of phylogeography (AVISE, 2000; ASSMANN & HABEL, 2009) provides important information for the understanding of historical and geographical relationships between populations of organisms. These data should be used as a basis for conservation decisions and actions, but this is made difficult by the frequent absence of a taxonomic and nomenclatural transcription of these findings. This may result from the limitations mentioned above put by the *Code* on the nomination of infraspecific taxa, but also from the fact that many researchers in phylogeography do not come from the discipline of taxonomy and lack a proper taxonomic "culture". Thus, instead of using the two infraspecific ranks recognized by the *Code*, they coined their own concepts and terms, such as those of "evolutionary significant unit" (ESU) or of "conservation management unit" (RYDER, 1986; MORITZ, 1994; FRASER & BERNATCHEZ, 2001). However, as these units do not correspond to formal taxonomic units bearing Latin nomina, they cannot easily be used for the protection of endangered taxa or their habitats, at least with the tools provided by the laws or regulations based on official texts or lists using such nomina. We think "phylogeographists" should also become "phylogeotaxonomists" and provide Latin nomina based on the rules of the *Code* for the units they recognize. This does not require to abandon the specific units such as ESU, but to distinguish the fact that these units designate *taxonomic categories* from the existence of formal units which correspond to standard *nomenclatural ranks*. In other words, a unit may well be defined *both* as an ESU from an evolutionary point of view and as a subspecies or an exerge (see below) from a nomenclatural point of view. The present paper provides such examples. Of course, to name taxa validly under the rules of the *Code*, taxonomists are bound to follow the latter and also its limitations in the number of ranks that can be used below species, arbitrarily limited to two, but hopefully modifications will be brought to this text to abandon these limitations (see DUBOIS, 2006*b*).

The *Code* provides the possibility to recognize and formally name taxa at a rank intermediate between species and subspecies. By similarity with the situation in other nominal-series (where the first rank below a primary rank starts by sub-: subclass, suborder, subfamily, subtribe, subgenus), it would be more logical to use the rank subspecies immediately below the rank species, and then infraspecies below (DUBOIS, 2006*a*), but to respect the *Code* we here interpolate one rank between species and subspecies. For taxa at this rank, rather than the unpalatable formula "aggregate of subspecies", we use VERITY's (1925) term *exerge*, as proposed and explained by BERNARDI (1980).

PHYLONOMY: SUPRASPECIFIC CLASSIFICATION

The numerous cladistic studies, mostly based on nucleic acid sequencing, that have been carried out in the recent years, often suggest rather detailed cladistic relationships between species, which can be expressed taxonomically and nomenclaturally through hierarchies, as discussed in detail by DUBOIS (2007*a*, 2008*d*). However, this transcription of cladistic hypotheses into classifications poses two kinds of problems, taxonomic and nomenclatural.

From a taxonomic point of view, most authors nowadays agree that only should be recognized taxa that appear, at a given stage of research, to correspond to "monophyletic" (sensu HENNIG, 1950) or better *holophyletic* (ASHLOCK, 1971) groups. This does not mean that all hypothesized holophyletic groups, i.e., all nodes in the trees, should be taxonomically recognized, for two distinct reasons.

The first one is that, even if we had a complete inventory of the animal species of the earth, and a completely resolved tree of relationships between them, it would not be appropriate to name all nodes, because this would result in very cumbersome and useless taxonomies that would be as uninformative as mere chaos. As a matter of fact, depending on the structure of the tree, up to $(n - 1)$ supraspecific taxa might be required to express taxonomically the cladistic relationships between all n species of the inventory (SZALAY, 1977: 363; DUPUIS, 1979: 45; DUBOIS, 2005*b*: 393).

The second problem results from the uncertainty of many of our results, which makes many of our trees labile. In most zoological groups, successive cladistic analyses provide different results, for various reasons (problems in vouchers' identification; different samplings of species and characters; different morphological or molecular methods; different algorithms for tree construction and for testing tree robustness and reliability). This does not mean that we should not use these successive hypotheses as temporary bases for the building of successive "working taxonomies" or *ergotaxonomies* (DUBOIS, 2005*b*), but that we should be aware of their temporary nature.

In this respect, it is useful to make the distinction between two kinds of information provided by cladograms. One is the recognition of rather small holophyletic clusters of closely related species, and the other is the respective and hierarchical relationships between these clusters. In well-studied zoological groups, after a certain time, a rather high robustness exists regarding the first kind of information, but this robustness may be much longer and difficult to obtain for the cladistic relationships between these clusters. Thus, several cladistic analyses of a zoological group (e.g., a family) composed of twelve species 1 to 12 may all agree in recognizing six specific clusters, A (1 + 2), B (3 + 4), C (5 + 6), D (7 + 8), E (9 + 10) and F (11 + 12), but disagree regarding the relationships between these clusters. Let us imagine for example that four successive analyses of this group provide the following results: (A(B(C(D + (E + F))))), (C(B(A(D + (E + F))))), (C(A + B)(D + (E + F))) and ((B(A + C))((D + (E + F))). A prudent, conservative and probably robust taxonomic transcription of these results would be: (1) to recognize A, B, C, D, E and F as taxa (e.g., genera); (2) to recognize (E + F), which comes back in all analyses, as a taxon G (e.g., a tribe); (3) in order to respect the hierarchical taxo-nomenclatural structure (see DUBOIS, 2008*d*), to recognize another tribe H for its sister-group, i.e., the genus D; (4) to recognize (G + H), which comes back in all analyses, as a taxon I (e.g., a subfamily), (5) to recognize three additional subfamilies, J, K and L, respectively for the genera A, B and C. This is because the mutual relationships between A, B, C and I are not yet clarified, which does not allow a robust taxonomic statement in the form of a hierarchy between them. This amounts to recognizing taxonomically all the robust specific clusters, but some only of the nodes of the trees obtained, those that appear constant in all analyses. In such taxonomies, taxa which are considered sister-taxa or members of an unresolved polytomy are *parordinate* (DUBOIS, 2006*b*) and must be given the same nomenclatural rank, which is just below that of their common *superordinate* taxon and just above that of their *subordinate* taxa if they exist (DUBOIS, 2008*d*).

Ranks as used in such hierarchies have a single purpose: that of providing unambiguous information on the *structure of the tree* used as a basis for the taxonomy, i.e., on sister-taxa and more remote relationships between taxa. They do not provide information of any kind, be it biological or historical (age), on the taxa referred to any particular rank. In other word, a family of bats and a family of bees are by no criterion *equivalent* (DUBOIS, 2007*a*, 2008*d*). However, this arbitrariness of ranks does not mean that allocation of ranks to taxa should be made blindly and without reflection. Three main constraints should be considered in this respect. The first one is that a few major "primary key ranks" should be considered universal and compulsory in all ergotaxonomies (DUBOIS, 2006*a*, 2007*a*, 2008*d*; KUNTNER & AGNARSSON, 2006): regnum, phylum, classis, ordo, familia, genus and species. All zoological organisms should be referable to taxa at these seven ranks, for simple reasons of indexation of the taxonomic information, and even if this entails a certain "taxonomic redundancy" in some cases (DUBOIS, 2007*a*, 2008*d*). The second constraint is that "major", i.e., "well-known" taxa, should be ascribed primary key ranks (such as order or family) and not secondary key ranks (such as legio or phalanx) or subsidiary ranks (such as suborder or subfamily) (for more details, see DUBOIS, 2006*a*). The third constraint is that particular attention should be given to the rank genus, because this rank plays a very special role in zoological nomenclature, being part of the binomen that designates each species. It is not enough to say that, to be recognized as a genus, a group should be "holophyletic" or should correspond to a "lineage" or a "clade" (for a criticism of the use of these terms, see DUBOIS, 2007*a*, 2008*d*), because knowing that a group includes all the descendants of an ancestral species does not in the least tell us whether this "clade" should be considered a genus, a tribe, a subgenus, a species-group or something else. We need additional criteria, which are not purely cladistic, but which take other information into account.

This matter was discussed at length by Dubois (1988*b*, 2004*b*), who suggested a series of criteria, including a mixiological one (see below), for the delimitation of genera. Frost et al. (2006) failed to discuss these criteria and did not provide any explanation on the criteria that they used to decide to recognize a "clade" either as a genus, a subgenus, a species-group, a tribe, a subfamily, a family or whatsoever. As a result, their generic taxonomy is highly unbalanced and poorly informative, as in some cases they grouped in the same genus several widely divergent "clades", whereas in other cases with similar species richness and diversity they adopted a much more divided generic taxonomy, presumably to respect "tradition" and "consensus". An immediate consequence of such a "methodology" is that this taxonomy fails to provide morphological diagnoses for many of the genera. We think the choice of the "level" where phylogenetic trees should be "cut" to insert the rank genus is an important matter because it has considerable consequences on the way eidonomy progresses. This choice should not be based on cladistic data alone (as a "clade" is a "clade", whatever its age, specific richness and diversity) but on other, non-cladistic criteria. Many field naturalists and taxonomists, when they observe or collect animals in the field, will try to identify them using monographs, revisions, keys, which very often are based on taxa of rank genus. Genera that include very divergent subgroups (e.g., the genus *Rana* as understood in many traditional works: e.g., Inger, 1954, 1966; Taylor, 1962) cannot be properly diagnosed morphologically and do not guide taxonomists for the recognition of new species, leading often to improper comparisons and taxonomic decisions. Given the present situation of taxonomy, where many new species await discovery, recognition and description before getting eventually extinct, using such "vague" genera is not doing a service to the study of biodiversity. We think zootaxonomists should only use genera that can be clearly defined by morphological diagnoses, usable by all field naturalists and zoologists.

Below, we afford the rank genus to well-defined and cladistically supported *holophyletic* groups of closely related species that share a number of characters (both apomorphies and plesiomorphies) providing morphological, but also sometimes behavioural and ecological, diagnoses. These species therefore share not only a general morphology but also a general "ecological niche" (Inger, 1958; Dubois, 1988*b*) and they are usually separated, according to these criteria, by a "gap" from the species of the closely related genera (Mayr, 1969; Dubois, 1988*b*). Within these groups, it is sometimes possible to recognize holophyletic subgroups that are not as strongly divergent and that may overlap in some characters, being often more difficult to diagnose morphologically or ethologically, and among which hybridization may remain possible. We think these groups should also be recognized as taxa, but at ranks lower than genus.

NOMENCLATURAL RANKS

In this paper we follow a nomenclature that fully respects the rules of the *Code*, particularly regarding the nomenclatural ranks allowed by this text. The *Code*, although it lists only five "standard" family-series ranks (superfamily, family, subfamily, tribe and subtribe), does not preclude the possibility to use further lower family-series ranks, as it accepts "*any other rank below superfamily and above genus that may be desired*" (Art. 35.1). We use this opportunity to recognize, below these five standard ranks, taxa at the rank infratribe, with the ending -*ITA*, as suggested by Dubois (2006*a*: 211). However, for supraspecific taxa below the rank genus, the *Code* only allows the use of two ranks, subgenus and "aggregate of species". Therefore, we refrained here from using ranks such as supergenus, infragenus or hypogenus, although we regret this impossibility (see Dubois, 2006*a*).

Below the rank genus, in agreement with other recent works in the **Urodela** (e.g. Parra-Olea et al., 2004; McCranie et al., 2008), we prefer to recognize first subgenera rather than "species-groups" or "species-complexes", as it is easier to designate a taxon by a single nomen than by a long expression using several terms, as shown by comparing the two sentences: (1) "In all species of *Pyronicia*, the dorsal colour is usually green with spots"; (2) "In all species of the *Triturus marmoratus* species-complex, the dorsal colour is usually green with spots". This is, in fact, the primary function of having a zoological nomenclature, rather than simply diagnoses, definitions or descriptions, or than numbers, codes or other non-verbal systems. Whereas computers use such coded systems, we, as humans, rather use words to designate things or concepts. Unfortunately, for additional subdivisions in the genus-series below the rank subgenus, taxonomists are bound to use such cumbersome designations (e.g., "*Triturus vulgaris* supraspecies"), because of the current limitations imposed by the *Code*. Anyway, the nomina of "intermediate" taxa such as subgenus or supraspecies do not need to be written every time a taxon is mentioned in the text. It may be useful to write the complete nomen of a taxon, with these nomina between parentheses, at the first mention of a taxon in a publication, or in a table like table 5 below, but then, in the text, a species needs only be mentioned by its binomen and a subspecies by its trinomen, without writing all these additional nomina (see below). In a non-taxonomic publication dealing with these taxa, the nomina at these intermediate ranks do not even need to be mentioned once.

Below the rank subgenus and above the rank species, the *Code* (Art. 6.2) offers the possibility to formally recognize taxa of a single rank, "aggregate of species". Their nomina, which belong in the nomenclatural species-series, may be interpolated between the genus-series nomen or nomina and the specific nomen, and the Principle of Priority applies to such nomina. To designate such taxa, rather than using multi-word formulae like "aggregate of species", "species-group" or "species-complex", the term *supraspecies* is available (Génermont & Lamotte, 1980, Dubois, 2006*a*) and is used here.

In a nomenclatural hierarchy as described above, four different situations can be distinguished regarding the number of subordinate taxa for each taxon. These situations can be described as four *categories of hypotaxy* (from the Greek *hupotaxis*, "dependence, submission, subordination"). As they correspond to different topologies of trees, with or without polytomies, they partly reflect the resolution of the tree and they can inform us about it.

(1) A given taxon may include only *one* immediately subordinate taxon, a situation which may be called *monohypotaxy* (from the Greek *monos*, "single, unique" and *hupotaxis*, "subordination")[1]. In such a case, the two successive ranks are clearly *redundant*, which means that

---

[1] The term *monotypic* is sometimes used in the taxonomic literature to designate a taxon that includes a single subordinate taxon or no subordinate taxon at all: thus the term "monotypic" is sometimes applied to designate a genus with a single species or a species that does not include subspecies. With this meaning, the term *monotypic* refers to a taxonomic concept. But this term is confusing as it is used in the *Code* in a different sense, to designate a nomenclatural concept, i.e., a mode of designation of onomatophore for a nominal taxon, either in the genus-series (Art. 68.3 and 69.3) or in the species-series (Art. 73.1.2). This confusion is illustrated for example by stating that a "monotypic" species (i.e., without subspecies) can well bear a nomen that relies on a

they do not provide distinct *taxonomic* information - but they may be useful for mere *nomenclatural* reasons (for more details, see Dubois, 2007*a*, 2008*d*).

(2) A given taxon may include *two* parordinate taxa of just lower rank, a situation which may be called *diplohypotaxy* (from the Greek *diploos*, "double" and *hupotaxis*, "subordination"). Taxonomically, this can be interpreted as meaning that a simple hypothesis of relationships between these two taxa exists. these two parordinate taxa can be considered as sister-taxa. Although this interpretation can be challenged by subsequent works, as long as it is not such a taxonomy appears like a "final" one.

(3) A situation of *polyhypotaxy* (from the Greek *polus*, "numerous" and *hupotaxis*, "subordination") occurs whenever *more than two* parordinate taxa are subordinate to a just superordinate taxon. The taxonomic meaning of this situation is unclear, as two different cases may account for it: (a) these parordinate taxa are the members of a still unresolved polytomy, which subsequent work can possibly help to solve, (b) an hypothesis already exists regarding the relationships between the members of the polytomy, but it was not implemented into the ergotaxonomy in order to limit the number of ranks of this taxonomy.

(4) Finally, a taxon may include *no* subordinate taxon, being the "terminal" lower taxon in a nomenclatural hierarchy. This situation which may be described as *anhypotaxy* (from the Greek *aneu*, "without" and *hupotaxis*, "subordination"). Given the current nomenclatural rules of the *Code*, this can occur only in two cases, when the "final" taxon is either a species or a subspecies.[2] By definition, all nomina at ranks above the rank species designate taxa that *include* at least one species, even possibly still unnamed and undescribed, so they cannot fall in the category of anhypotaxy.

Whereas mono-, diplo- and anhypotaxy are expected to be observed in a well-resolved tree and taxonomy, polyhypotaxy may reflect partial irresolution of a tree. Therefore, an ergotaxonomy with a high rate of polyhypotaxy is unsatisfactory and clearly requires further work. This does not mean however that an ergotaxonomy without polyhypotaxy would be definitive and perfect, as inclusion of new taxa and new data may lead to change it.

Because of the nomenclatural parsimony resulting from the Principle of Coordination (see Dubois, 2008*d*), less nomina then taxa are necessary to express a hierarchical taxonomy, especially at higher ranks because more ranks can be recognized in the family-series than in the other nominal-series. This can be measured by a *nomenclatural parsimony ratio*: NPR = number of distinct nomina / number of taxa. The terms "distinct nomina" mean that the different avatars of a nomen that may exist at different ranks within a nominal-series (e.g., family and its hyponymous subfamily, genus and its hyponymous subgenus, etc.), are different *morphonyms* but are the same *nomen*, with the same onomatophore, author and date (Dubois, 2000). The ratio NPR is lower when nomenclatural parsimony is higher. The more a taxonomy is balanced and resolved, and the lowest its rate of polypotaxy, the lowest its NPR is.

---

holophoront fixed by original designation, or on symphoronts among which not lectophoront was ever designated, i.e., two situations that do not correspond to "monotypy" in the sense of the *Code*. This confusion is avoided by using the terms *monohypotaxy* and *anhypotaxy* for the taxonomic concepts and *monophory* (Dubois, 2005*b*) for the nomenclatural concept. The existence of this confusion, that has been entertained until now in all the literature, is an additional reason for rejecting the use of the term "type" and terms based on this root in taxonomy and nomenclature, beside those given by Dubois (2005*b*).

[2] This is another situation for the use of the traditional but misleading term *monotypy*: see infrapaginal note 1 above.

THE USE OF HYBRIDIZATION DATA IN TAXONOMY

Hybridization experiments, which were very "fashionable" in the first half of the 20th century and until the seventies, have stopped being so in our "all-cladistic" age, but it is to be hoped that future taxonomists will again get interested in such data, as they are very rich in information for the understanding of the evolution of zoological groups (see DUBOIS, 1988*b*). This particularly applies to works on the family *SALAMANDRIDAE*, in which for several decades these data have been considered of utmost importance for establishing taxonomic groups (e.g., in the genus *Triturus* as traditionally understood), but largely ignored in the recent years.

Hybridization data can be useful at two different levels in taxonomy, in eidonomy for the recognition of taxonomic species and in phylonomy for the recognition of taxonomic genera.

A few recent authors proposed a concept of taxonomic species as a "lineage", according to which, as soon as two groups of individuals are liable to produce together fertile hybrids, they should be referred to the same species: "*in spite of appearances, when two interbreeding organisms taken in apparently diverging lineages leave fertile offspring, there is no reason to conclude the existence of distinct species. If this indeed occurs, no new branch has appeared in the phylogenetic tree. Whatever the definition of species may be, considering 'interpecific hybridization' is conceptually inconsistent.*" (SAMADI & BARBEROUSSE, 2006: 515-516). We fully and strongly disagree with such a statement, which is at complete variance with the use of the category species in most zootaxonomic publications until now. To drastically "redefine" nowadays the "species concept" along such guidelines would introduce extreme confusion and chaos in the discussion on these matters which is already very complex, and is certainly not to be recommended! If these idea had to be followed, then almost all ducks in the world (family *ANATIDAE*), which hybridize freely in captivity but rarely in nature, would belong in a single taxonomic species, and the same would be true in innumerable other cases over the whole of zoology (see DUBOIS, 1988*b*).

As a matter of fact, the concept envisioned by these authors is not that of "species", at least as has been understood by the overwhelming majority of authors for two centuries (i.e., a set of individuals which *in nature* breed *freely* together), but another concept, designating all the individuals susceptible of producing together, even in artificial conditions, viable hybrids. This concept was called *coenospecies* by TURESSON (1929) and *syngameon* by CUÉNOT & TÉTRY (1951, 455) (see BERNARDI 1980: 396, 398). This is indeed a useful concept, but not for the taxonomic category of species. It was called upon (DUBOIS, 1982, 1988*b*) to help defining a particular taxonomic category of rank genus or "genion" (DUBOIS, 2007*a*, 2008*d*, 2009*b*). The term coenospecies being misleading (suggesting that it is a "kind of species") and syngameon being preoccupied by an homonymous term designating another category (LOTSY, 1918), this taxonomic concept can be known as *coenogenion* (DUBOIS, 2007*a*) or *coenogenus*, better *mixogenion* or *mixogenus* (from the Greek *mixis*, "mixing, sexual intercourse" and *genos*, "descent, race, family").

Contrary to what some believe, crossability between species is not a *character* of each of these species but a "relational taxonomic criterion" (DUBOIS, 1988*b*) or *relacter* between them (DUBOIS, 2004*b*). Its use does not rely on its bearing information on cladistic relationships, but on its measure of the overall genetic divergence between the genomes of two species after their separation. The ability of two half-genomes to build together a hybrid adult organism through the very complex processes of ontogeny cannot be due to convergence or chance, but to the conservation of common or very similar *mechanisms of genetic regulation*, and this is a much more sensible and meaningful measurement of "genetic distance" between them than any index based on *structural similarity of genomes* (DUBOIS, 1988*b*).

A mixogenus is a taxon of nomenclatural rank genus that includes at least *some* taxonomic species among which adult diploid true hybrids (not polyploid, gynogenetic or androgenetic offspring) are known to have been produced, either in natural or in artificial conditions, between specimens belonging to two distinct taxa, although in nature the latter behave as normal species (e.g., mayrons or kleptons). This does not mean that *all* species included in a mixogenus should be hybridizable, because of the characteristics of interspecific hybridization in animals, in particular its asymmetry, non-transitivity and quick disappearance between sympatric species (for details, see DUBOIS, 1988*b*), but that any other species subsequently discovered to have successfully crossed with a member of the mixogenus (and also in some cases other related species) should be included in the latter. Such a taxonomic concept is fully compatible with the requirement that, to be recognized as a taxon of nomenclatural rank genus, a group should be holophyletic. It just provides an additional criterion for placing the "bar" where to insert the "genus level" among various hierarchically related "clades". DUBOIS (2004*b*) provided detailed explanations and recommendations in this respect. It should be stressed that, to be usable, the cross should have resulted in *adult* diploid true hybrids, but that the latter may be fertile or sterile, for reasons explained in full detail by DUBOIS (1988*b*).

The use of hybridization data at the "species level" is different, as briefly tackled above. Many cases are known of "good species" that rarely, occasionally or even regularly hybridize in nature without having to be considered "conspecific". Mayrons connected in nature by "hybrid zones", like *Bombina bombina* and *Bombina variegata*, are not rare in amphibians. The important point here is the structure and dynamics of the hybrid zone. Very schematically, if in the latter a bidirectional gene flow exists between the two entities, with symmetric bilateral genetic introgression that tends to homogenize both gene pools as a single one, they belong in the same mayron (possibly as two distinct submayrons). In contrast, if this zone acts as a (possibly leaky) barrier between both taxa, allowing them to remain clearly distinct and "recognizable" (morphologically, molecularly or both), they should be considered distinct mayrons (DUBOIS, 1977, 1998*a*).

We used these guidelines to support some of the taxonomic changes presented below. Many cases of hybridization, whether natural or artificial, have been documented in the *SALAMANDRIDAE* in the last century. Regarding the crossability criterion at the nomenclatural level of genus, the requirement imposed by the use of the mixogenus taxonomic category is that no adult hybrid (whether fertile or infertile) be known to have been produced between two species referred to different taxonomic genera. This clearly applies to most known cases of successful interspecific hybridization in this family, which occurred between taxa referred below to the same genus. Two problematic cases, between the genera *Pleurodeles* and *Tylototriton* on one hand, and among the modern European newts on the other, are discussed in more detail below. At the specific level, a number of subspecies recognized below are known to be connected by hybrid zones which seem to allow free bidirectional gene flow between them. In several other cases, hybrids are known to exist, or to have existed, in nature between two entities, but the available data do not suggest that a free symmetric gene flow exists between them, and we recognize them as distinct species. This is the case in particular in several groups of modern European newts, as briefly discussed below.

TAXOGNOSES

Whereas nomina of taxa are not "defined" but "attached" to taxa through their onomatophores (DUBOIS & OHLER, 1997, DUBOIS, 2005*b*, 2007*a*, 2008*d*), taxa are indeed "defined" (not "discovered", as stated by some, because taxa are concepts, not objects). There are several ways of "defining" the taxa as recognized by a taxonomy. Most of them belong in two major categories: (1) "phenetic definitions" such as the "diagnoses" traditionally used in taxonomy, and (2) "phylogenetic definitions" (DE QUEIROZ & GAUTHIER, 1990, 1994). These different kinds of definitions do not play the same role or give the same information and it is useful to provide several of them altogether when defining a taxon (see e.g. the example in DUBOIS, 2007*a*: Appendix). This is what we do below, so we here define the terms we use.

We use the new term *taxognosis* (from the Greek *taxis*, "putting in order" and *gignosko*, "I know") as a general term for any *definition of a taxon*. Taxognoses are of two main sorts: (1) a *physiognosis* (from the Greek *physis*, "nature, inborn quality" and *gignosko*, "I know") is a taxognosis that provides *characters* considered to allow a non-ambiguous identification of the taxon, irrespective of any cladistic hypothesis; (2) a *cladognosis* (DUBOIS, 2007*a*; from the Greek *klados*, "branch" and *gignosko*, "I know") is a "phylogenetic definition" of the taxon, i.e., a taxognosis that is associated with a cladistic hypothesis. Both these categories contain subcategories.

(1a) A *diagnosis* (traditional term in taxonomy, from the Greek *diagnosis*, "distinction, discrimination") is a physiognosis based on "character states" or *signifiers* (ASHLOCK, 1985) that are considered to be differential for the taxon, i.e., shared by all members of the taxon and absent in all non-members.

(1b) An *idiognosis* (from the Greek *idios*, "one's own, particular, proper" and *gignosko*, "I know") is a physiognosis based on signifiers that are considered to provide a brief description or characterisation of a taxon, including both diagnostic (differential) signifiers and signifiers shared with other taxa.

(2a) An *apognosis* (DUBOIS, 1997, from the Greek *apo*, "from, away from" and *gignosko*, "I know") is a cladognosis based on signifiers that are considered to be shared by all members of the taxon and absent in all non-members, and that are considered, on the basis of a cladistic analysis and hypothesis, to be autapomorphic for the taxon. Such cladognoses have also received the long and cumbersome designation of "apomorphy-based definitions" (DE QUEIROZ & GAUTHIER, 1990).

(2b) A *coinognosis* (DUBOIS, 2008*d*; from the Greek *koinos*, "common, kindred", and *gignosko*, "I know") is a cladognosis based directly on the hypothesized cladistic relationships between taxa. Such cladognoses, which received no designation by DE QUEIROZ & GAUTHIER (1990) and their followers, are of four kinds. Two of them, first defined by DE QUEIROZ

& GAUTHIER (1990), are based on explicit formulations of *hypotheses of cladistic relationships* between organisms or taxa, and on statements about "common ancestors".

(2ba) A "node-based definition" (DE QUEIROZ & GAUTHIER, 1990), or more briefly a *rhizognosis* (DUBOIS, 2008*d*; from the Greek *rhiza*, "root", and *gignosko*, "I know"), is a coinognosis defining a taxon as including all organisms or taxa stemming from the most common ancestor of two specified organisms or taxa.

(2bb) A "branch-based definition" (DE QUEIROZ & GAUTHIER, 1990), or more shortly a *caulognosis* (DUBOIS, 2008*d*; from the Greek *kaulos*, "stalk", and *gignosko*, "I know"), is a coinognosis defining a taxon as including all organisms or taxa sharing a more recent common ancestor than with another taxon.

As a matter of fact, statements about "common ancestors" (which in most cases are unknown and hypothetical) are not indispensable to provide non-ambiguous definitions of taxa, at least within the frame of a given cladistic hypothesis and ergotaxonomy. Both these later definitions can be reformulated sparing the *designation* of these unknown ancestors, by using the concept of monophyly sensu HENNIG (1950) or holophyly (ASHLOCK, 1971): a holophyletic taxon includes an ancestor and all its descendants. Such coinognoses are based only on the *inclusion* of organisms or taxa in the taxon, sometimes combined with the *exclusion* of other organisms or taxa, without explicit statements about the ancestors. As it relies on the concept of holophyly, it makes sense only when applied to a given cladistic hypothesis. These two kinds of coinognoses, used e.g. in DUBOIS (2006*a*, 2007*a*: Appendix) have remained until now unnamed.

(2bc) An "inclusion-based definition" or more shortly an *entognosis* (from the Greek *entos*, "within, inside" and *gignosko*, "I know"), is a coinognosis defining a taxon as the *least inclusive holophyletic* taxon (i.e., based on a cladistic hypothesis) *including* one or several organisms or taxa. The mention of "least inclusive" is important here, as without this mention the coinognosis would apply to the whole animal kingdom, not to say the whole tree of life. Although formulated differently, in practice an entognosis is strictly equivalent to the rhizognosis based on the same included organisms or taxa.

(2bd) A "bidirectional-based definition" or more shortly an *entexognosis* (from the Greek *entos*, "within, inside", *exo*, "outside", and *gignosko*, "I know"), is a coinognosis defining a taxon as the *most inclusive holophyletic* taxon (i.e., based on a cladistic hypothesis) *including* one or several organisms or taxa and *excluding* one or several other organisms or taxa. Although formulated differently, in practice an entexognosis is strictly equivalent to the caulognosis based on the same included and excluded organisms or taxa.

Such definitions are used in fact for the allocation of nomina to taxa within the frame of nomenclatural rules. Entexognoses apply to the situation of allocation of nomina to taxa of the three lower nominal-series recognized by the *Code*, which rely on onomatophores only (combined with the Principle of Coordination). They also correspond to the situation, described in the rules proposed by DUBOIS (2006*a*) for class-series nomenclature, of choronyms, i.e., nomina that apply to orotaxa, being based both on onomatophores and onomatostases. In contrast, in these rules, entognoses correspond to the situation of nesonyms, that apply to metrotaxa and are based on onomatophores alone (but without a Principle of Coordination). This rather complex point is not developed further here as it is beyond the scope of the present work (see DUBOIS, 2007*a*, 2008*d*). The cladognoses of taxa given in DUBOIS (2007*a*: Appendix) are entexognoses.

In the present work, for each taxon erected or "resurrected", we provide three different taxognoses: an entexognosis, a diagnosis (in a table) and an idiognosis.

COMMENTS ON NOMENCLATURE

ZOOLOGICAL NOMINA SHOULD BE SHORT AND SIMPLE

Many recently published cladistic analyses imply taxonomic changes. When carried to their logical conclusion, new cladistic hypotheses, derived from such analyses, lead to new supraspecific classifications, and often require the creation of new nomina for newly defined taxa. The *Code* only provides a few rules and recommendations for the mode of formation of zoological nomina, and these rules are not very binding. As far as the *Code* is concerned, taxonomists are basically "free" to coin every nomina they like. Does this almost complete "freedom" mean that they should not follow any guidelines in this respect?

As a matter of fact, in the recent years, as well exemplified in the **AMPHIBIA**, this "freedom" has resulted in a clear trend to create long, unpalatable nomina. Such nomina are often created on the basis of complex etymologies, derived from Latin, Greek or modern terms or roots combined together. Such long and complex nomina may appear to some more "serious" or "scientific" than short and simple ones, but they are not necessary. The *Code* does not in the least require the use of complete roots or "correct etymologies" for scientific nomina — which would be very difficult indeed as there are not and cannot be rules for a "correct" derivation of a nomen from a Latin or Greek etymology, or, even worse, for a "correct latinisation" of non-Latin terms (for more details, see DUBOIS, 2007*b*).

The *Code* does not either "forbid" the creation of long nomina. In its *Appendix B*, it simply "*recommends*" that nomina "*should be euphonious and easily memorable, and should not be liable to confusion with those of other taxa of any rank, or with vernacular words*". The criterion of "euphony" is of difficult application, as the same term may sound more or less "euphonious" according to the culture or language spoken by a person. However, it seems clear that a brief nomen composed of simple syllables with only two or three letters each (one or two consonants and a single vowel) will be considered "simple and euphonious" by all, whereas more complex structures may not. Despite the absence of rule in this respect in the *Code*, NG (1994) aptly criticized the creation of very long nomina, and gave some extreme examples, such as the generic nomen *Siemienkiewicziechinogammarus* Dybowski, 1926 (14 syllables, 29 letters) and others, that were invalidated by the International Commission on Zoological Nomenclature (ICZN) for being a potential cause of "*greater confusion than uniformity*" (ANONYMOUS, 1929: 1). Beside the length proper, i.e., the number of letters, a nomen may be characterized by its phonetic complexity, i.e., its number of syllables or vowels. This is so because in classical Latin all vowels were pronounced separately (like in modern Spanish or Turkish), so that a nomen like *Hyalinobatrachium*, which contains 8 vowels, must be considered to consist in 8 different syllables (*Hy-a-li-no-ba-tra-chi-um*).

When coining new nomina, many zoologists seem to forget the basic purpose of these terms. Scientific nomina are not descriptions, diagnoses, statements on the characters, distribution or other characterisations of the taxa they designate. They are not models, evolutionary, phylogenetic or genetic theories about the hypothesized origin of these taxa. They are not praises for their authors (see Dubois, 2008*a*), for the discoverers of the taxa or for the persons to whom they may be dedicated. They are just neutral *labels* meant at designating *unambiguously* and *universally* a given taxon *within the frame of a given taxonomy*, i.e., allowing the automatic pointing to the taxa recognized by taxonomists at a given stage of their research. These labels allow storage and retrieval of the information accumulated in taxonomies (Mayr, 1969), but they are not meant at expressing this information by themselves. As such, nomina are fully *meaningless* and should remain so. This is why the *Code* expressly states that availability of nomina "*is not affected by inappropriateness*" (Art. 18), and allows a new generic or specific nomen to be "empty of meaning", for example for being "*an arbitrary combination of letters provided this is formed to be used as a word*" (Art. 11.3).

Famous examples of "empty nomina" include the crustacean generic nomina *Anilocra*, *Canolira*, *Cirolana*, *Conilera*, *Nelocira*, *Nerocila*, *Olencira* and *Rocinela*, all created by Leach (1818: 347-351) as anagrams of the surname "Carolina" or "Caroline": they are all short, euphonious, and fully appropriate for zoological genera. The same system could appropriately have been or be followed in many other genera. Thus, if the genus amphibian genus *Bufo* had to be dismantled (a debated question not discussed here), why not use for the new taxa anagrams of this nomen, like "Bofu", "Fobu" or "Fubo", or similar but slightly different nomina like "Bufa", "Bufus" or "Fufo" (the latter used already twice, but inadvertently and therefore as an incorrect subsequent spelling, by Fang & Zhao, 1992: 86), rather than coining long unpalatable nomina?

It is certainly praiseworthy for an author to have cared for a new nomen to be derived from an identified etymology (but then this should be done correctly: see Dubois, 2006*c*, 2007*c*), but this is much less important than the nomen being grammatically correct regarding its number (singular or plural according to the rank, see Dubois, 2009*a*) and being short, euphonious in all languages and "*easily memorable*".

Scientific nomina are not an aim in themselves, but *tools* that are used in various contexts. Once coined, a new nomen will appear not only in taxonomic and phylogenetic publications, but also in all the scientific and non-scientific literature, in titles, official documents and lists, etc., published and distributed over the whole planet, that will deal with the organisms it designates. As such, it is much more important that nomina be short, simple and euphonious in all languages of the world than "full of meaning" and "strictly formed" from an etymological point of view. Because of the *rule of priority* and of the *nomenclatural founder effect* on which the nomenclatural rules are based (Dubois, 2005*d*), a nomen, once created, cannot be changed by subsequent authors and can be so only by a special intervention of the ICZN using its Plenary Powers, a very rare and heavy procedure. If it is the first one available for the taxon it designates, this nomen will have to be used by all authors who will deal with this taxon. When they are used in non-specialized literature, long and complex nomina are certainly not a good "publicity" for taxonomy, especially in our times when this scientific discipline is facing difficulties (Wheeler et al., 2004; Padial & De la Riva, 2007). When coining new nomina, zootaxonomists should therefore care for those being short and simple

This is particularly true for nomina designating "exceptional" or famous organisms, which will have to be mentioned hundreds of times in the non-specialized literature, on the web and in various other medias. This also applies to generic nomina that are at their creation, or are likely to become later, the basis for familial nomina. These considerations were clearly not taken into account by some authors who created long nomina for such recent discoveries.

The trend to coin long and unpalatable nomina is particularly obvious in the class **Amphibia**, being even stronger for fossil taxa. Do we really need in zoological nomenclature specific nomina like *thoracotuberculatus* (8 syllables, 19 letters) or *acanthidiocephalum* (8 syllables, 18 letters), generic nomina like *Amphignathodontoides* (8 syllables, 20 letters) or *Saevesoederberghia* (9 syllables, 18 letters), familial nomina like *Pseudophlegethontidae* (10 syllables, 22 letters) or *Calyptocephalellidae* (9 syllables, 20 letters) or higher taxa nomina like **Hydatinosalamandroidei** (11 syllables, 22 letters) or **Palaeobatrachomorpha** (9 syllables, 20 letters)? Taxonomists should also certainly avoid coining particularly highly repetitive nomina like *Ogalalabatrachus* (7 syllables, 16 letters). Although such nomina are indeed a very small minority among the many available nomina of **Amphibia**, they tend to become more and more common, at least in some taxonomic groups. This can be exemplified by the generic nomina listed by Frost et al. (2006: 175, 213-214) in the families *Bufonidae* and *Salamandridae* as recognized by them. The 50 nomina listed in their *Bufonidae* have from 4 (*Bufo*) to 16 letters (*Dendrophryniscus* and *Melanophryniscus*), with a mean of 11.3 and a median of 11.5. The 18 generic nomina listed in their *Salamandridae* have from 6 (*Cynops*) to 15 letters (*Lyciasalamandra*), with a mean of 10.7 and a median of 11.0, but if the 20 nomina of fossil genera of this family (Estes, 1981, Venczel, 2008) are added, the maximum among the 38 nomina raises to 18 letters (*Cryptobranchichnus* and *Palaeosalamandrina*) and the mean to 11.6, the median remaining 11.0. The difference in the median number of letters between these two families is not significant (Mann-Whitney *U* test, $U = 928$, $P = 0.852$). In both families, a clear trend for an increase in the length of nomina over time since 1758 can be observed (fig. 1).

In contrast, the 37 nomina of *Ranidae* listed by Frost et al. (2006: 248) only have from 3 (*Amo*) to 13 letters (*Pseudoamolops*), with a mean of 8.5 and a median of 8.0. The difference between the *Bufonidae* and *Ranidae* is highly significant (Mann-Whitney *U* test, $U = 705$, $P < 0.001$), and that between the *Salamandridae* and the *Ranidae* as well (Mann-Whitney *U* test, $U = 258.5$, $P < 0.001$). No clear trend for the increase in the length of nomina over time can be observed in the *Ranidae* (fig. 1). This important difference is not due to chance. It is clearly related to the fact that rather numerous generic nomina of *Ranidae* were coined rather recently, in particular in a paper by Dubois (1992), with the clear intention to make them short and simple – a point that has escaped the attention of most authors who have commented this work (e.g., Inger, 1996). In contrast, the recent creation of many generic nomina of *Salamandridae* and especially of *Bufonidae*, by several authors, was clearly made without any concern for this problem.

In our opinion, for the sake of communication with the whole community of zoologists and non-zoologists, this increase in the length of generic nomina in many families should not be encouraged, and future nomina to be coined should be short and simple. This is the case of the new nomina proposed below. As a rule of thumb, we would suggest that specific, generic and higher nomina should include a maximum of 8-12 letters (preferably less) arranged in

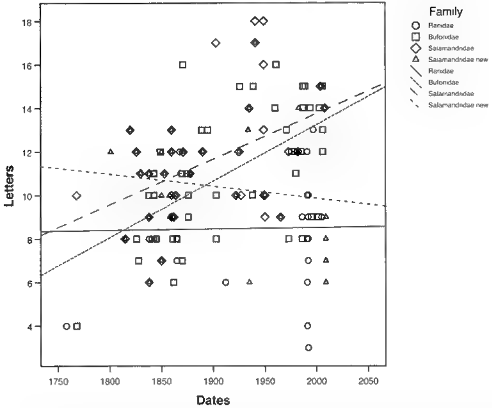


Fig. 1. Numbers of letters in the genus-series nomina of three amphibian families (Bufonidae, Ranidae, Salamandridae) as recognized in Frost et al. (2006), with addition of the fossils in the Salamandridae (see text), as well as in the ergotaxonomy of the family Salamandridae adopted at the end of the present work ("Salamandridae new"). Each genus is plotted according to its number of letters and publication date, and regression lines over time of the number of letters are shown for the four groups of data.

4-5 syllables as defined above (preferably less), the latter being mostly composed of one or two consonant(s) and one vowel, as this is more likely to be euphonious in all or most languages. This should probably not become a "rule" of the *Code*, but it would be a useful addition to its "recommendations". This rule of thumb can be used as a guideline by all taxonomists working nowadays.

How can nomina be shorter and simpler, without completely losing their etymology and "meaning"? There are several ways to do so, four of which at least can be highlighted.

(1) The use of more than two roots for a nomen should be avoided, as this always results in long nomina (*Allomesotriton*, *Brachytarsophrys*, *Pseudhymenochirus*).

(2) For coining nomina based on two or more different roots, nothing in the *Code* requires to combine the *complete* roots. Such nomina can validly be created by combining

parts only of the roots, as exemplified by many generic nomina of **AMPHIBIA** (e.g., *Afrana*, *Grobina*, *Kurixalus*, *Megophrys* or *Telmalsodes*), including several ones recently created in the **URODELA** (see e.g. PARRA-OLEA et al., 2004; MCCRANIE et al., 2008). Generic nomina like *Lyciasalamandra*, *Nasikabatrachus* or *Paramesotriton* are unnecessary long The virtually same nomina would aptly have been coined as "Lyciandra", "Nasikus" or "Paratriton" (none of which is preoccupied).

(3) Among several roots that carry the same message, preference should be given to the shortest and simplest one e.g., in **AMPHIBIA**, "rana" instead of "batrachus" or "bufo" instead of "phrynus".

(4) An efficient way to reduce the length of nomina is to avoid adding long, useless endings to their basic root: thus, a specific nomen based on the name of a locality, region or country can well be coined by simply using the name of this place as it is, placed in apposition to the generic nomen, hence invariable. This avoids adding long endings in *-ensis*, *-ense*, *-cola*, *-icus*, *-ica*, *-icum*, *-ianus*, *-iana*, *-ianum*, etc. Additionally, this precludes potential grammatical mistakes of agreement in gender in case of transfer of the species to another genus. We think this should become a recommendation of the *Code*, and that its current Recommendation 11a, stating that "*An unmodified vernacular word should not be used as a scientific name*" should be suppressed The recent decades have witnessed an unprecedented increase in the number of specific nomina ending in *-ensis*, especially in some countries, which provoke a real indigestion to people who are sensible to the aspect and length of nomina, and this should certainly change We may be special, but we much prefer short specific nomina based on local geographical terms like *Aubria masako* (6 letters), *Colostethus roraima* (7 letters), *Phrynopus carpish* (7 letters), *Rana diuata* (6 letters) or *Rana rara* (4 letters) to unpalatable ones like *Bolitoglossa guaramacalensis* (15 letters), *Crotaphatrema tchabalmbaboensis* (17 letters), *Megophrys wuliangshanensis* (16 letters), *Scutiger mokokchungensis* (15 letters), or *Hyalinobatrachium guairarepanensis* (16 letters, not to mention the 17 letters of the generic nomen[1]).

A final recommandation that we would like to offer regarding the formation of new nomina concerns the grammatical gender of nomina of new subgenera. All the history of taxonomy since 1758 has shown a general trend in the progressive upgrading of ranks of taxa: what was a species in LINNAEUS (1758) has now often become a genus or a family, what was a family in LATREILLE (1825) has often become an order or a class, etc This trend has accompanied the drastic increase in the number of named species and in our knowledge concerning the organisms. This upgrade in ranks poses no theoretical problems for taxonomy, as ranks do not carry any biological, evolutionary or other information and are purely arbitrary, just expressing the hierarchical structure of taxonomy and sister taxa relationships (DUBOIS, 2007*a*, 2008*d*) However, one of the results of this trend is that, regularly, subgenera or species-groups are elevated to the rank of genera. A particularity of zoological nomenclature is that specific epithets must agree in grammatical gender with their generic substantives. When a species is transferred from a genus to another whose nomen has a different grammatical gender, the ending of the specific nomen, if it is an adjective or a participle, must often be modified, and some zoologists have difficulties doing this, so that mistakes are regularly published in this respect One possible way to avoid such errors is to care for new subgeneric nomina having the same grammatical gender as that of the nomen of the genus We cared for this below, but of course, when a subgeneric nomen is not a newly coined one but is transferred from another taxa or "resurrected", nothing can be done in this respect as this nomen cannot be modified

NUCLEOSPECIES DESIGNATIONS FOR GENERA

Nucleospecies ("type species") *designations* for genera are crucial acts in zoological nomenclature. Because the nomenclatural system of the *Code* is based on ostension using onomatophores and not on intensional definitions of taxa (see Dubois, 2005*b*, 2007*a*, 2008*d*), a genus nomen applies to any genus-series taxon including its nucleospecies, whatever diagnosis or definition of the taxon designated by this nomen had been given originally. Before working on the generic taxonomy of any zoological group, the first thing to do is therefore to identify the nucleospecies of all nominal genera referred to this group. We did this for the family *SALAMANDRIDAE* and we then realized that, just like for the family *RANIDAE* a few decades ago (Dubois, 1981), among various nomenclatural errors repeated uncritically in the literature, a number of nominal genera still had no nucleospecies, and could therefore not be properly allocated to taxa. We therefore designate nucleospecies for all of them below.

The rules of the *Code* regarding nucleospecies designations require to follow a strict "*order of precedence*" among several possibilities (Art. 68): (1) original designation, (2) original monophory; (3) absolute tautonymy; (4) Linnaean tautonymy; (5) subsequent designation, (6) subsequent monophory. As defined by the *Code*, the situation (2) of original monophory should be strictly understood as meaning "including a single valid species", irrespective of the fact that this species may or not include several subspecies or synonyms (see below under *Neurergus*). These six possibilities are the only ones recognized by the *Code* for nucleospecies designation. This excludes for example designation "by implication" (see below under *Triturus*). The existence of an order of precedence among these possibilities means e.g. that if (1) applies, then (5) cannot apply, etc. The cases (3) and (4) are rare and apply only to old generic nomina published by Linnaeus or just subsequent workers. In the family *SALAMANDRIDAE*, only the cases (1), (2) and (5) are encountered. Attention has to be given to the fact that the choice of a nominal species for subsequent designation is limited to the "*originally included species*" of the nominal genus. As defined by the *Code* (Art. 67), these nominal species are either "*those included in the newly established nominal genus or subgenus*" (Art. 67.2.1) or, if no nominal species was originally included in it (which is acceptable until the end of 1930, Art. 13.3), "*the nominal species that were first subsequently and expressly included in it*" (Art. 67.2.2). This means that if a nominal genus was created without included species, any species can be subsequently included into it, *even if described and named after this nominal genus*. This precision is given here because we use this possibility below. Another important precision is that the "*originally included species*" cover *all* the *nominal* species listed by the original author as belonging in the genus, not only those considered valid by this author, i.e., also including the synonyms.

According to the *Code*, whenever several nomina are linked by a *relation of neonymy* (i.e., involving an archaeonym and one or several neonyms subsequently proposed for it), all these nomina have by definition the same nucleospecies, whether this species was first designated as nucleospecies for the archaeonym or for any of its neonyms (Art 67.8). This rule also has consequences in the generic nomenclature of the SALAMANDRIDAE.

Finally, it must be stressed that, by definition, a neonym can have only one archaeonym. It is impossible under the *Code* to consider that a nomen has been proposed as a neonym for two or more distinct nomina (except in the improbable case where they would already all be linked by a relation of neonymy), as this would result in the same nomen having several distinct onomatophores and appearing in several distinct synonymies. A given nomen must be ascribed to a single synonymy, because, if it was indeed the synonym of several distinct nomina, this would mean that the latter also are synonyms [3]. Therefore, whenever a new nomen is published with a statement that it is meant at "replacing" two or more older nomina, this must be understood nomenclaturally as a double operation: (1) a subjective synonymisation of these two or more older nomina, (2) the creation of a new nomen for a new taxon and the inclusion of the two or more older synonyms in its synonymy. In the case of a new generic nomen thus proposed, its nucleospecies has to be established on the basis of the nominal species included in the new genus hence created.

THE NOMENCLATURAL STATUS OF WEBSITES DEALING WITH AMPHIBIA

Several websites are now available online dealing with the **AMPHIBIA**, including three very famous and useful ones, *Amphibian Species of the World* (*ASW* below) [http // research.amnh org/herpetology/amphibia/], *AmphibiaWeb* (*AW*) [http //amphibiaweb.org/] and the *Global Amphibian Assessment* (*GAA*) [http.//www.globalamphibians.org/]. Many batrachologists, zoologists and laymen use these three sites to find information about amphibians, and a tendency has developed in the recent years to quote these sites in scientific papers and to include their addresses in reference lists. This is problematic because websites, being labile in their content, cannot constitute permanent scientific bibliographic references (DUBOIS, 2003*b*). The same website can be consulted at different dates, and, except for a few persons who "followed" daily the site or stored its data in a way or another, there exists no possibility today to know what was the content of this site at the given date, even if this date is provided with the reference (which is not always the case) Thus for example, in the book of HUTCHINS et al (2003), two of the sites mentioned above are cited in reference lists of some contributions, as having been consulted at the following dates: *ASW* on 12 April 2002 (p 94), 19 April 2002 (p. 130), 8 May 2002 (p. 117), 15 June 2002 (p. 88) and 19 November 2002 (p. 444), and *AW* on 12 April 2002 (p. 94), 8 May 2002 (p. 383) and 19 November 2002 (p. 443). It is impossible today for most "normal" users to have access to the original documents referred to by these "references". The latter may be useful to find a website providing some information, but this information changes with time, so they are useless as "references" to "publications" in fact, they simply amount to mentioning a "personal communication", a letter or a manuscript by a colleague, and as such they should not appear in bibliographical reference lists (DUBOIS, 2003*b*, 2004*a*).

---

[3] There exists a rare exception to this situation: a species-series nomen given to a specimen that later is shown to be an interspecific hybrid must be referred to the synonymy of both its parental species. Two specific nomina are in this case in the SALAMANDRIDAE: *Triton blasii* de l'Isle du Dreneuf, 1862, and *Triton trouessarti* Peracca, 1886. Both were created for specimens that were hybrids between *Triturus cristatus* (Laurenti, 1768), and *Triturus marmoratus* (Latreille, 1800), so these two nomina should stand in both their synonymies, but with a clear indication that they apply to interspecific hybrids, e.g. using the sign ×.

Although these sites always appear on top in any "Google search" and although many people think that they are more of less "official" and have the strong status of basic, unavoidable references, they are not. The *GAA* site is the only one to be in some way "official", as it presents the categories of threats of amphibian taxa as recognized by an international organization, the International Union for the Conservation of Nature (IUCN). The other two sites are only private sites, documented and maintained by private teams of people or even by a single individual. They are certainly very interesting and helpful to everybody, but the information they contain should never be taken for granted and uncritically accepted as valid or authoritative. This is clearly shown by the fact that all three websites present different, sometimes incompatible information, regarding the accepted phylogeny and taxonomy, the valid nomina of the taxa, the distribution of the species, etc.

This can be illustrated easily In early November 2008, one of us (AD) just clicked on the name of the first country in the lists of countries of these three sites, which happens to be Afghanistan. The three sites provided different lists of amphibian taxa occurring in this country, with different nomina and distributions· 6 species in *GAA* (*Batrachuperus mustersi*, *Bufo stomaticus*, *Euphlyctis cyanophlyctis*, *Hoplobatrachus tigerinus*, *Paa sternosignata*, *Rana ridibunda*), 9 species in *AW* (*Bufo latastii*, *Bufo oblongus*, *Bufo pseudoraddei*, *Bufo stomaticus*, *Bufo variabilis*, *Euphlyctis cyanophlyctis*, *Paa sternosignata*, *Paradactylodon mustersi*, *Rana ridibunda*) and 11 species in *ASW* ("*Bufo*" *olivaceus*, "*Bufo*" *stomaticus*, *Chrysopaa sternosignata*, *Euphlyctis cyanophlyctis*, *Hoplobatrachus tigerinus*, *Paradactylodon mustersi*, *Pelophylax ridibundus*, *Pseudepidalea oblonga*, *Pseudepidalea pewzowi*, *Pseudepidalea pseudoraddei*, *Pseudepidalea turanensis*). The only nomen which appears identical in the three lists is *Euphlyctis cyanophlyctis*. The differences result either from simple nomenclatural disagreement, or from real taxonomic divergences, or from use of different distributional data on the species (in particular incorporating unpublished data, especially in *GAA*). Any user of these websites should therefore make his/her opinion about the information they provide, which often requires the recourse to external references. The contents of these sites should therefore never be considered as a "norm" that should necessarily be followed (e g , regarding the valid nomina of taxa) [4].

As concerns zoological nomenclature, these websites (as well as other similar ones) pose a particular problem· the new nomenclatural acts that they inevitably contain are not nomenclaturally available and should not be quoted in paper publications As defined by the *Code* (Art 8), to qualify as a "*published work*", a publication "*must have been produced in an edition containing simultaneously obtainable copies by a method that assures numerous identical and durable copies*" (Art 8 1 3), and, if "*produced after 1999 by a method other than printing on paper*", it "*must contain a statement that copies (in which it is published) have been deposited in at least 5 major publicly accessible libraries which are identified by name in the work itself*" (Art 8 6). These conditions exclude all works that are "published" only online, without a printed version

Nomenclatural acts are of various kinds, e g *correction* of an incorrect original or subsequent spelling; *new combination* or more generally *new onymorph*; *change of ending*

---

[4] Ironically, after these lines had been written the third of the three websites mentioned above (*GAA*) closed (apparently in December 2008) and its content was transferred to another website (http://www.iucnredlist.org/amphibians We did not check whether the transfer was complete or not and whether it implied content modifications or not but this points to the relevance of our analysis above pointing to the "lability" of websites and their inappropriateness as permanent bibliographic references.

following a change of generic allocation for a species-series nomen or of rank for a family-series nomen, *designation* of a lectophoront (lectotype) for a species or of a nucleospecies for a genus; etc. Strictly speaking, most of these actions (e.g., the creation of a new combination) do not have "nomenclatural authors" but only *first-users* (DUBOIS, 2000). Nevertheless, many checklists, catalogues and revisions provide the first-users of all onymorphs in their synonymies or *logonymies* (DUBOIS, 2000): their authors should then refrain from crediting the new onymorphs to these websites, because they are nomenclaturally unavailable there, i.e., "non existent" in zoological nomenclature. Any author who mentions an onymorph as having appeared in one of these sites becomes in fact, in strict nomenclatural terms, its first-user.

As tackled above, in our present discussion regarding salamandrid nomenclature, we are particularly concerned by the problem of nucleospecies designations for all nominal taxa that have not yet received such a designation. In this respect, the website *ASW* is particularly unreliable. The first version of this work, published as a book (FROST, 1985), contained a very high rate of errors and omissions (from 0.8 to 90.9 % according to the kind of information, with a mean of 33.3 % over 18 items) that required the publication of a long list of corrections (DUBOIS, 1987*b*-*c*). Most of these corrections have been incorporated in the website, but many other "new" mistakes, especially errors in the synonymies, have been added, so that this website cannot be used blindly as a solid nomenclatural reference for amphibians.

Generic synonymies in *ASW* present information on past nucleospecies designations, but also sometimes unpublished data. Such new designations, or original "identifications", of nucleospecies that appear in this site are nomenclaturally unavailable and should not be cited in serious taxonomic works. In other cases, *ASW* acknowledges the fact that no nucleospecies designation already exists for some generic nomina, and includes these nomina in several synonymies (those of the genera containing the originally included species of the nominal genus), which is highly confusing and nomenclaturally impossible, as shown above. The only proper allocation of a generic nomen that still does not have a nucleospecies is as an "incertae sedis" at the level of the higher taxon (tribe, subfamily, family, etc.) that is considered to include all its possible nucleospecies (e.g., all its originally included species).

Another related mistake consists in considering that a given generic nomen can be a neonym for several distinct older genera altogether, which is impossible for reasons explained above. Such nomina are in fact brand new nomina, and, if no subsequent nucleospecies designation has taken place, they must also be considered "incertae sedis".

Finally, attention should be called to the fact that, besides these erroneous statements, some of the basic information given in *ASW* concerning some nucleospecies designations is incorrect, as exemplified below in several cases in the salamandrids.

For the time being, Art. 8 of the *Code* clearly states that a new nomen or nomenclatural act only published online has no nomenclatural availability, which is quite clear. Plans exist however to render available some nomina and acts published online *under particular conditions* (ANONYMOUS, 2008). Understanding these conditions may be easy for members of the ICZN or "professional taxonomists", but not so for all laymen and unspecialized users of the web, who will be tempted to consider as "nomenclaturally available" any nomen or nomenclatural act gathered on the web. It is therefore easy to predict that, if these projects were indeed implemented, a period of nomenclatural confusion (if not chaos) will open, regarding which nomina, lectophoront or nucleospecies designations, are available and valid.

The nomina created by de la Cepède (1788*a-b*)

One of the major functions of the *Code*, as stated in its *Preamble*, is to "*promote stability and universality in the scientific names of animals*". The ICZN, which is in charge of updating the *Code* and of dealing with problematic cases, often claims to care for "nomenclatural stability" and for this reason, in the recent years, has given more weight than in the past to "usage" against the Principle of Priority, which poses various problems that need not be discussed here (see Dubois, 2005*a*, 2008*c*). However, in some recent cases, this Commission has indeed taken decisions that go in the exactly reverse direction, for reasons that are difficult to understand, but which may have more to do with the egos of some persons than with a concern for "nomenclatural stability". Thus, in the same period when this Commission "suppressed" a family-series nomen to "protect" a completely obscure tribe nomen that had been used *only 16 times* in zoological nomenclature since 1758 before the application for its conservation (Dubois, 1994; Anonymous, 1997), the ICZN suddenly decided (Anonymous, 2005) to deny nomenclatural availability to all the amphibian and reptilian nomina created in the very famous books by de la Cepède (1788*a-b*), quoted thousands of times since their publication, despite clear warnings against "*a rigid application of the Rules to old, well-known zoological works*" (Bour & Dubois, 1984) and despite "*strong objection to the structure and content of the application*" by one Commissioner[5]. There is no doubt that, if all nomina in these two books had to be suppressed because of a few questionable species nomina not written under binominal form, although clearly included in genera, then many other nomina that have been in universal use for more than two centuries should also be "suppressed". Bour & Dubois (1984) gave the examples of the works of Schlosser (1768) and Boddaert (1770*a-b*, 1772*a-b*), and an even more caricatural one can be mentioned (Dubois, 2005*b*: 426): the book of Laurenti (1768), universally used as the starting point for the nomenclature of **Amphibia** and **Reptilia**, contains specific nomina that are fully unacceptable under the rules of the *Code*, such as "*Chamaeleo bonae spei*", "*Coluber vipera anglorum*", "*Vipera Francisci Redi*", "*Vipera Mosis Charas*" or "*Constrictor rex serpentum*". Certainly "suppressing" this book would in no way "*promote stability* [illegible] *in the scientific names of animals*", but the same was entirely true for de la Cepède's (1788*a-b*) books.

Be it as it may, we think that, to avoid the progressive implementation of a "nomenclatural chaos" which would no doubt result from all authors following "their own rules" (see examples in Dubois, 2006*c*, 2007*c*, 2008*d*), zootaxonomists should care to follow strictly the *Code* and the decisions of the ICZN even when they were not in favour of the latter. Even if an overwhelming majority of them, if they had been consulted, would certainly not have agreed with the "suppression" of these books by a small team of "nomenclature specialists", European herpetologists will now have to change their habits and stop using de la Cepède's nomina. In many cases, these nomina can be replaced by identical nomina used in Bonnaterre (1789), in a book that was largely derived from de la Cepède's (1788*a-b*) books, but in a few other cases this is not possible, when Bonnaterre had changed de la Cepède's nomina, which clearly results in nomenclatural instability.

---

[5] As usual in the recent years (but not in the past: see Dubois, 2005*b*: 367-369), the deliberations of the ICZN being "secret", the international community of zoologists was not informed of the nature of these "*strong objections*" nor of the replies which no doubt were given to them in order to convince the Commissioners not to share them.

This is not the case, fortunately, in the *Salamandridae*. Two species-series nomina coined by de la Cepède (1788*b*), that have been used in all checklists of species of this family and in all faunae of Europe or European countries for more than two centuries (e.g., Mertens & Wermuth, 1960*b*, Thorn, 1969; Thorn & Raffaëlli, 2001, Raffaëlli, 2007), must now be credited to Bonnaterre (1789). *Salamandra terrestris* and *Salamandra tetradigitata*. In the latter case, the change is only one of authorship: the onomatophore (a single specimen kept in the Paris Museum under number MNHN 4658, Thireau, 1986: 76) and the onymotope (Vesuvius, Italy) are not modified, as Bonnaterre (1789: 62) clearly stated that he had borrowed his description from de la Cepède (1788*b*). But the same does not apply to the nominal species *Salamandra terrestris*. For this species, de la Cepède (1788*b*: 194) considered a very wide distribution, including most of Europe ("*tant de pays de l'ancien monde, et même à de très-hautes latitudes*"), and did not state the origin of the specimens observed by him in the "*Cabinet du Roi*" (now the Paris Museum), so no precise onymotope was originally identified. Eiselt (1958: 136) designated Normandy (France) as "terra typica restricta", but this onymotope restriction, followed by all authors until now, not being associated with a lectophoront or neophoront designation, is nomenclaturally void (Dubois & Ohler, 1995: 146, 1997: 312). Bonnaterre (1789: 62), when he redescribed the species under the nomen given to it by de la Cepède (1788*b*: 456), precised that he had written his description on the basis of two specimens he had observed on 11 October 1788 at Saint-Geniez en Rouergue (now Saint-Geniez-d'Olt, Aveyron, France, **valid onymotope**). Therefore, *Salamandra terrestris* Bonnaterre, 1789 has a precise onymotope, which is distinct from, and actually quite far from (about 600 km in straight line) that until now accepted for *Salamandra terrestris* de la Cepède, 1788. Very fortunately, both localities are included in the distribution currently accepted for the subspecies *Salamandra salamandra terrestris*, so this nomen remains the valid one for the same taxon.

THE NOMENCLATURAL STATUS OF THE URODELAN GENERIC NOMINA CREATED BY RAFINESQUE (1815)

When it became consensual among batrachologists that the "*Triturus vulgaris* species group" should be recognized as a distinct genus, two different nomenclatural solutions to this problem were offered. Montori & Herrero (2004: 51) proposed to use the generic nomen *Lissotriton* Bell, 1839, whereas Litvinchuk et al. (2005: 317) proposed to use the nomen "*Lophinus* Rafinesque, 1815". However, as noted by Schmidtler (2004: 25), the latter nomen is a gymnonym, unavailable in zoological nomenclature. This is also true for Rafinesque's (1815) nomina "*Megapterna*" and "*Palmitus*", but not for his nomen *Triturus*, contrary to the statement by Schmidtler (2004: 23), followed by Speybroeck & Crochet (2007). This deserves a few explanations.

In all his publications, and particularly in his 1815 work, Rafinesque rigorously used a very precise way of proposing his new generic nomina, with two distinct situations that have different nomenclatural consequences nowadays (Dubois, in preparation). All his new nomina were followed by the letter "R.", which means that he claimed authorship for them. But then some only were immediately followed by another generic nomen. This mode of notation, very common in taxonomic works at the beginning of the 19th century (see e.g. Dubois, 1987*d*), means that the new nomen was proposed as a neonym for the following one. However, some other new nomina in Rafinesque (1815) were neither followed by another generic nomen, nor by the nomina of included species, nor by a diagnosis or description of the genus: such nomina are indeed gymnonyms, unavailable in zoological nomenclature.

Rafinesque (1815: 78) listed five genera in his family *Tritonia*, as follows: "G. 1. *Triturus* R. *Triton* Dum. 3 [for 2] *Salamandra* Lac. 3 *Palmitus* R. 4. *Lophinus* R. 5. *Meînus* R. [sic]". There is a single, straightforward, interpretation of this presentation: (1) he recognized the genus *Salamandra* as used by de la Cepède (1788*b*: 456), which is in fact a subsequent usage of the generic nomen *Salamandra* Laurenti, 1768; (2) he proposed the neonym *Triturus* for the generic nomen *Triton* as used by Duméril (1806), which is in fact a subsequent usage of the generic nomen *Triton* Laurenti, 1768: this neonym is fully available in zoological nomenclature; (3) he proposed three gymnonyms, "*Lophinus*", "*Meinus*" and "*Palmitus*": being devoid of any description, indication or mention of nominal species included in the taxon, these three nomina are unavailable in zoological nomenclature.

Fitzinger (1843: 34) designated *Triton cristatus* Laurenti, 1768 as nucleospecies of *Triton* Laurenti, 1768. Thus doing, he also designated the nucleospecies of all the neonyms proposed by subsequent authors for the latter nomen for its being preoccupied by *Triton* Linnaeus, 1758 (Mollusca), which are four in number: *Triturus* Rafinesque, 1815; *Molge* Merrem, 1820; *Oiacurus* Leuckart, 1821; and *Tritonella* Swainson, 1839 (a nomen ignored by most authors until now: e.g., García-París et al., 2004). All these nomina are objective synonyms and the valid nomen of the genus including *Triton cristatus* Laurenti, 1768 is *Triturus* Rafinesque, 1815.

Despite their being nomenclaturally unavailable, the three other nomina created by Rafinesque (1815) need nucleospecies, in order to be allocated to the synonymy of a single valid nomen (see below). Fortunately, despite the absence of diagnoses and included species, clues exist for the designation of these nucleospecies.

First of all, we are guided by the fact that one of these three nomina was "validated" later on, by Gray (1850: 27), who recognized a genus *Lophinus* and provided a diagnosis for it, thus making it nomenclaturally available. Although Gray (1850: 27) expressly credited this nomen to "Rafinesque", the latter is not the nomenclatural author of the nomen. The *Code* expressly states that the author of a nomen is not the person who coined it but "*the person who first publishes it (...) in a way that satisfies the criteria of availability*" (Art. 50.1). Gray (1850: 26-28) referred two nominal species to his new genus *Lophinus*, *Salamandra punctata* Latreille, 1800 and *Salamandra palmata* Schneider, 1799. None has been subsequently designated as nucleospecies, so that proper taxonomic allocation of this nomen has remained impossible until now. We hereby designate the nominal species *Salamandra punctata* Latreille, 1800: 31 as the nucleospecies of both "*Lophinus*" Rafinesque, 1815 and *Lophinus* Gray, 1850 (**new nucleospecies designations**). These two nomina are therefore now linked by an objective synonymy, and they are both invalid objective **new synonyms** of *Lissotriton* Bell, 1839 (nucleospecies, *Salamandra punctata* Latreille, 1800, by subsequent designation of Fitzinger, 1843: 34).

As for the other two gymnonyms created by Rafinesque (1815), they were not "validated" by subsequent authors, but they may be so or might be so in the future. This may be useful in case of need to recognize additional genus-series taxa within the group of European newts, e.g. for taxa at rank subgenus or even at lower ranks such as infragenus, should the *Code* later allow the use of such ranks. In such cases it will be useful to know the nucleospecies of Rafinesque's (1815) nominal taxa, in order to use the same nucleospecies for the same nomen once validated by publication of a diagnosis, definition or description. For this reason we here designate nucleospecies for these two gymnonyms.

By itself, the nomen "*Palmitus*" Rafinesque, 1815 (not mentioned in *ASW*) suggests that it was intended for the palmate newt. We hereby designate the nominal species *Lacerta helvetica* Razoumowsky, 1789: 111, its now valid nomen, as nucleospecies of this gymnonym (**new nucleospecies designation**). The latter is not "revalidated" here, but could be useful for "revalidation" if this species had to be taxonomically separated, as some level of the genus-series, from the other species of *Lissotriton*. For the time being, this gymnonym has to stand in the synonymies of the latter nomen (**new synonym**), both as genus and subgenus.

As for the nomen "*Meinus*" Rafinesque, 1815 (listed in *ASW* as a synonym of both *Lissotriton* and *Triturus*), we indeed "revalidate" it below, for a subgenus of *Lissotriton*.

PROPOSED TAXONOMIC CHANGES IN THE FAMILY *SALAMANDRIDAE*

We identified taxonomic problems at different levels in the family *Salamandridae*. After a brief presentation of these problems, we offer new taxonomic and nomenclatural proposals for this family. With the data currently available, all the taxa we recognize appear to correspond to robust holophyletic groups.

SUBFAMILIES

Several authors in the past have recognized two major groups in the *Salamandridae*: the "true salamanders" (*Salamandrinae*) and the "newts" (*Pleurodelinae*). However, recent works, based on both molecular (Larson, 1991, Titus & Larson, 1995, Larson et al., 2003, Montori & Herrero, 2004, Weisrock et al., 2005, 2006, Steinfartz et al., 2007, Zhang et al., 2008) and skeletal (Venczel, 2008) data, suggest that the genus *Salamandrina*, and possibly the poorly known fossil genus *Archaeotriton*, should be recognized as a third distinct lineage (Raffaëlli, 2007: 150, 343), the "spectacled salamanders". This is acknowledged below by the erection of a third subfamily (for which the nomen *Salamandrininae* is already available) for these two genera.

TRIBES, SUBTRIBES AND INFRATRIBES

Within subfamilies, the situation is rather simple concerning the relationships within the "true salamanders" (*Salamandrinae*). All recent molecular studies (Titus & Larson, 1995, Veith et al., 1998, Weisrock et al., 2001, 2006, Steinfartz et al., 2007, Zhang et al., 2008) confirm the existence of two main holophyletic groups within this subfamily: *Salamandra* and

Lyciasalamandra (that may be called "stout salamanders"), and *Chioglossa* and *Mertensiella* ("slim salamanders"). These two groups are here taxonomically recognized as tribes.

The situation is more complex regarding the "newts" (*Pleurodelinae*). They have often been considered to consist in two major groups. The first one, called "primitive newts" by Zhang et al. (2008), includes the Palaearctic genera *Pleurodeles*, *Tylototriton* and *Echinotriton* and related fossil genera, whereas the second one, unnamed by Steinfartz et al. (2007) and Zhang et al. (2008) but that may be called "modern newts", includes the other Palaearctic and the two Nearctic genera (Estes, 1981; Hayashi & Matsui, 1989; Titus & Larson, 1995; Larson et al., 2003; Montori & Herrero, 2004; Veith et al., 2004, Frost et al., 2006; Weisrock et al., 2006, Steinfartz et al., 2007, Zhang et al., 2008). These two groups can be taxonomically recognized as two tribes, whose valid nomina are *Pleurodelini* and *Molgini* (Dubois, 1985).

Recent works (Hayashi & Matsui, 1989; Weisrock et al., 2001, 2005, 2006, Montori & Herrero, 2004, Steinfartz et al., 2007, Zhang et al., 2008) suggest the existence of several holophyletic subgroups within the latter tribe. We propose to recognize taxonomically these finer subdivisions as subtaxa within the *Molgini*.

The first dichotomy within the "modern newts" is between the two Nearctic genera *Notophthalmus* and *Taricha* and all the other genera. The North American group, the "New World newts" of Steinfartz et al. (2007) and Zhang et al. (2008), already identified by Hayashi & Matsui (1989), is strongly supported in several recent analyses (Weisrock et al., 2005, 2006, Frost et al., 2006, Steinfartz et al., 2007, Zhang et al., 2008), and is here recognized as a new subtribe. The second subtribe *Molgina*, the "modern Eurasian newts" of Steinfartz et al. (2007), is also well supported (Frost et al., 2006, Weisrock et al., 2006; Steinfartz et al., 2007; Zhang et al., 2008). It contains several groups that appear holophyletic in all recent analyses, but their mutual relationships are not yet fully clarified, which does not allow to establish a taxonomic hierarchy between them (see above). Pending the resolution of these relationships, we only recognize some members of this polytomy as three taxa of the same family-series rank, as infratribes of the *Molgina*.

The first infratribe, the "Corso-Sardinian newts" of Zhang et al. (2008), consists in a single genus, *Euproctus*, as redefined by Carranza & Amat (2005). This distinctive holophyletic group, already recognized by Caccone et al. (1994, 1997), was nested among the group including all other European genera in several recent works (Montori & Herrero, 2004, Carranza & Amat, 2005, Steinfartz et al., 2007), but appeared as the sister-group of all other European newts in the analyses of Weisrock et al. (2006) and Zhang et al. (2008).

The second infratribe, the "modern Asian newts" of Steinfartz et al. (2007) and Zhang et al. (2008), includes *Cynops* and all other East Asian genera of the subtribe *Molgina*. It has been well supported as a holophyletic group in several studies using different methods (Hayashi & Matsui, 1989, Titus & Larson, 1995, Chan et al., 2001, Frost et al., 2006, Weisrock et al., 2006, Steinfartz et al., 2007; Zhang et al. 2008), but its relationships with the other European genera is not consensual among them.

The third infratribe, the "modern European newts" of Zhang et al. (2008), includes all the remaining European newt genera. Although it came out as a well supported holophyletic group in the analysis of Zhang et al. (2008), this group appeared as paraphyletic in all other recent analyses (Carranza & Amat, 2005, Weisrock et al., 2006; Steinfartz et al., 2007) and may have to be dismantled when the cladistic relationships among its genera and with the East Asian ones, which are still controversial, are better understood. Given the uncertainties that remain regarding the cladistic relationships between its genera, we consider it premature to recognize formal taxonomic groupings above genus within this infratribe (see also below the problems posed by the data on hybridization).

Genera and subgenera

Stout salamanders

This group contains a high number of species and is likely to be dismantled in the future. Steinfartz et al. (2000), Escoriza et al. (2006) and Weisrock et al. (2006) provided convincing molecular evidence for the existence of at least six holophyletic groups in this complex. We here treat them taxonomically as subgenera. Although this may appear premature to some, a major reason for our doing so is to avoid the repetition of the unfortunate creation of long unpalatable nomina like *Lyciasalamandra* for these taxa. We therefore propose below short, "compressed" nomina for the subgenera of *Salamandra*.

New World newts

The molecular data of Weisrock et al. (2006) provide strong support for the existence of two holophyletic groups in each of the two Nearctic genera *Notophthalmus* and *Taricha*. We here recognize two subgenera in each of these genera.

Modern Eurasian newts

Within this group of the "true newts", several recent works based on molecular cladistic data have resulted in important taxonomic changes regarding the traditional European genera *Triturus* and *Euproctus*, with recognition of several distinct genera (Montori & Herrero, 2004, García-París et al., 2004, Carranza & Amat, 2005; Litvinchuk et al., 2005). These taxonomic decisions are supported by the recent analysis of Zhang et al. (2008). We follow them here although we have reservation about the rank genus given to several of the newly recognized taxa (see below). Anyway, if this generic taxonomy is adopted, simple taxonomic consistency and homogeneity then requires also bringing changes to the taxonomy of the traditional East Asian genera *Cynops* and *Paramesotriton*.

Based on cranial characters, Zhao & Hu (1984, 1988) recognized three species-groups in the genus *Cynops*: a Japanese one, with the species *pyrrhogaster* and *ensicauda*, and two Chinese ones, with all other species. Chan et al. (2001) suggested that this genus is paraphyletic, its Japanese species being more closely related to the genera *Paramesotriton* and *Pachytriton* than to its Chinese species, and that, if these results were confirmed, "*an appropriate taxonomic resolution would be to recognize the genus* Hypselotriton *(Wolterstorff, 1934), as a valid taxon containing at least* cyanurus *and* wolterstorffi" (Chan et al., 2001: 1005). Weisrock et al. (2006: 380) did not find support for the paraphyly of *Cynops*, but they wrote that "*this grouping is not well supported by either Bayesian or parsimony analyses*". Their results are congruent with the holophyly of both the Japanese and Chinese groups of this genus, which was again confirmed by Steinfartz et al. (2007) and by Zhang et al. (2008). Here, we restrict the genus *Cynops* to the Japanese species and we place all Chinese species in the genus *Hypselotriton*. This genus is here understood with a wider extension than in several recent Chinese publications (e.g., Fei et al 1990, 2005, 2006; Ye et al., 1993; Fei, 1999) where it accommodated only the species *wolterstorffi*, whereas all other species of this group were maintained in *Cynops*.

Following Zhao & Hu (1984, 1988), two well-identified groups at least can be recognized in this genus. the *wolterstorffi* group (with the species *chenggongensis*, *cyanurus* and *wolterstorffi*) and the *orientalis* group (with *orphicus* and *orientalis*). We recognize these two groups as subgenera of *Hypselotriton*. The nomen *Pingia* Chang, 1935 is available for the second subgenus. This nomen is based on the nucleospecies *Pachytriton granulosus* Chang, 1933. The holophoront of this species being lost, its identity has long been uncertain: some authors (e.g., Thorn, 1969; Thorn & Raffaëlli, 2001) considered it as a synonym of *Cynops orientalis*, others (e.g., Fei et al., 2006, Raffaëlli, 2007) as a synonym of *Pachytriton labiatus*, and others (e.g , Ye et al., 1993; Zhao & Adler, 1993) simply ignored it. This species was recently rediscovered in the field by Hou et al. (2009), who provided a redescription, measurements and photographs. Based on these new data, we agree with Chang (1936) in considering these specimens as belonging in a species close to, although distinct from, *Hypselotriton orientalis* (David, 1875), and not in the genus *Pachytriton*. As stated by the latter author, this is most likely also the species collected by Pope in 1921 in Anhwei and considered by Schmidt (1927: 555) as a "terrestrial stage" of *Triturus orientalis*. *Hypselotriton granulosus* (**new combination**) is distinguished from *Hypselotriton orientalis* by its being slightly larger (total length up to 96 mm versus 90 mm in *orientalis*), its very tuberculate dorsal skin (versus slightly granular in *orientalis*), with minute glands on the dorsum and the head, its orange red spots along each side (no spots or very few on the sides of *orientalis*) and its big orange-red blotches on the ventral surface (smaller red blotches in *orientalis*) Both species occur in Zhejiang.

The genus *Paramesotriton*, as traditionally understood, is also heterogeneous. The recently described species *laoensis* shows strong both morphological and well-supported molecular divergence from all other species of the genus and also to the genus *Pachytriton*, appearing as the sister-group to the cluster of these two genera (Weisrock et al , 2006. 378) or to the genus *Pachytriton* (Zhang et al , 2008). This indeed suggests that it "*should not be placed in the genus* Paramesotriton" (Weisrock et al , 2006: 380) We here refer this beautiful and distinctive species to its own genus, for which we provide a nomen. Within the remaining group, both morphological (Chan et al , 2001) and molecular (Weisrock et al , 2006) data suggest that the species *caudopunctatus* represents a distinct holophyletic group, sister to the cluster of the remaining species. We here place it in a distinct subgenus, for which a nomen is already available (Raffaëlli, 2007: 128)

In the European genus *Triturus*, two "species-complexes", *cristatus* and *marmoratus*, have long been recognized, and they are supported by all recent analyses (Macgregor et al , 1990; Mikulíček & Piálek, 2003, Montori & Herrero, 2004, Carranza & Amat, 2005; Weisrock et al , 2006, Steinfartz et al., 2007) We recognize them taxonomically below as two subgenera, for which nomina are already available Similarly, we recognize as subgenera the two "clades" (northern and southern) within the genus *Neurergus*, separated since 11 Mya according to Steinfartz et al. (2002).

In the genus *Lissotriton*, WEISROCK et al. (2006) identified two distinct groups, one with *Lissotriton boscai* and one with all other species, which we here recognize as subgenera. PECIO & RAFIŃSKI (1985) pointed to the absence of "whip and wave" during the male nuptial dance of *Lissotriton boscai*, whereas these behaviours are present in all other *Lissotriton* species, although very attenuated in *Lissotriton italicus*. The genus *Ichthyosaura* also lacks whip and wave, and this absence is clearly a plesiomorphic character.

A particular problem would be posed by the implementation of the mixogenus concept, as defined above, in the group of the modern European newts. For most of the 20th century, many authors realized articificial hybridization experiments between all the species that were then placed in a single genus *Triturus* (see subcomplete lists of references in MANCINO et al., 1978 and in MACGREGOR et al., 1990: 339-340). According to these works, adult hybrids were obtained between various species, not only of the same genus according to the current generic taxonomy of these newts, but also belonging to different genera: *Ichthyosaura* and *Lissotriton* (SCHREITMÜLLER, 1910; WOLTERSTORFF, 1925: 280, 289; BATAILLON, 1927; BATAILLON & TCHOU SU, 1932; LANTZ, 1934; PARISER, 1935, 1936; MANCINO et al., 1976; MACGREGOR et al., 1990), *Ichthyosaura* and *Ommatotriton* (MACGREGOR et al., 1990), *Ichthyosaura* and *Triturus* (BATAILLON, 1927; BATAILLON & TCHOU SU, 1932; PARISER, 1935, 1936), *Lissotriton* and *Triturus* (POLL, 1909; WOLTERSTORFF, 1909*a-b*, 1910, 1911, 1925: 279; BATAILLON, 1927; BATAILLON & TCHOU SU, 1932; PARISER, 1932, 1935, 1936; HAMBURGER, 1935; MANCINO et al., 1976, 1977, 1978, 1979; MACGREGOR et al., 1990); and *Lissotriton* and *Ommatotriton* (WOLTERSTORFF, 1925: 279; MACGREGOR et al., 1990). For the oldest works, no data are available on the ploidy and characters of these specimens, that would allow to ascertain that they were indeed diploid adult hybrids, but such data exist in the recent works. Thus, MANCINO et al. (1977) reported in detail about diploid adult hybrids between *Lissotriton meridionalis* and *Triturus carnifex*. Certainly this question should be studied again, but, given the current disinterest of taxonomists for hybridization (DUBOIS, 1998*a*), we may have to wait for a while until fresh detailed data are available.

If all the "intergeneric" adult hybrids liable to be produced, at least in artificial conditions, between these groups, proved to be real diploid hybrids, adopting the mixogenus concept would require to downgrade all four genera *Ichthyosaura*, *Lissotriton*, *Ommatotriton* and *Triturus* to the rank of subgenera of a single genus *Triturus*. Furthermore, if the cladistic relationships within modern newts presented by WEISROCK et al. (2006) and ZHANG et al. (2008) were confirmed, the genera *Calotriton* and *Neurergus* should also be treated as subgenera of *Triturus*, for simple reasons of cladistic consistency (see DUBOIS, 2004*b*). The current subgenera recognized below in some of these genera should then be downgraded to the rank of supraspecies (or later of infragenera if this rank is subsequently authorized by the *Code*). This would contradict the recent trend which has led to the upgrading of the species groups of *Triturus* to separate genera. The taxonomist community is a very conservative one, and changes take time to be eventually accepted. It is unlikely that time is ripe for the salamander taxonomists of today to lump again what they have been splitting in the recent years. For this reason, and also because detailed information on the ploidy and chromosomal complement of most of these "intergeneric" hybrids is still wanting, we do not implement these consequences of the reported crosses in our taxonomy, but we wish to stress that this would not at all be shocking and inacceptable. It would not exactly amount to coming back to the generic taxonomy that has long prevailed for European newts, as it would require the inclusion of a few additional groups in the genus *Triturus*. It would simply result in a change of rank for the taxon recognized by RAFFAËLLI (2007) as the supergenus *Triturus* and below as the infratribe *MOLGITA*, but without modifying its content and taxognosis, nor those of its included taxa

Primitive newts

Within the genus *Tylototriton*, two well-supported holophyletic groups have been identified by WEISROCK et al. (2006) They correspond to the *asperrimus* and *verrucosus* species groups as recognized by FEI (1999) and FEI et al. (2005, 2006), and they are supported by clear behavioural differences. They are recognized here as two subgenera

In this group also, a particular problem would be posed by the use of the mixogenus concept. FERRIER et al. (1971) reported having obtained hybrid specimens between females of *Pleurodeles waltl* and males of *Tylototriton verrucosus*. FERRIER & BEETSCHEN (1973) later reported that some of these hybrids of both sexes (numbers not given) reached the adult stage. In particular, the males had nuptial pads. However, they failed to obtain reproduction from these hybrids. Since that date however, no adult hybrid between these genera was reported, although these newts have been raised in captivity by several amphibian breeders.

On the basis of these successful crosses, DUBOIS (1982, 1987*a*) suggested that *Tylototriton* and *Echinotriton* should be considered subgenera of *Pleurodeles*. Whereas at the time of WOLTERSTORFF (1925) or LANTZ (1947) such a suggestion would probably have been followed, it is interesting to note that, since 1982, not one author seems to have adopted this taxonomic proposal, despite the comments of BUCCI-INNOCENTI et al. (1983) on the use of artificial hybridization results in taxonomy. For this reason, which in our opinion reflects rather the "conservatism" of the taxonomic community mentioned above, than a clear "genus concept" alternative to that of mixogenus, we here maintain these taxa at the rank of genera. However, we suggest that in the future the possibility to downgrade *Pleurodeles* and *Tylototriton* to the rank of subgenera of a single genus *Pleurodeles* should be seriously considered Besides, as *Pleurodeles* seems to be the sister-taxon of the group *Echinotriton* + *Tylototriton* (WEISROCK et al , 2006; ZHANG et al., 2008), this would imply also considering *Echinotriton* as a third subgenus of *Pleurodeles* for mere reasons of cladistic consistency (see DUBOIS, 2004*b*), and the latter genus should perhaps include also some of the fossil genera currently recognized in the tribe *PLEURODELINI* (see table 5) If *Tylototriton* was to be downgraded to the rank of a subgenus of *Pleurodeles*, the two subgenera here recognized in *Tylototriton* should be downgraded to the rank of supraspecies, respectively *verrucosus* for *Tylototriton* and *asperrimus* for the new subgenus defined below. Hopefully also, in the future, the *Code* will allow for the use of a rank infragenus, which would allow to have a more expanded hierarchy of genus-series ranks below genus and might make it easier to abandon the "genera" *Tylototriton* and *Echinotriton*

SUPRASPECIES, SPECIES, EXERGES AND SUBSPECIES

We presented above the criteria that we use to recognize taxa of rank species. In some situations, this leads us to elevate some former subspecies to the rank species, quite in the line of the suggestions of HIGHTON (2000).

In a few cases, we use additional ranks around the rank species to account for rather detailed relationships between species and subspecies inferred from recent data in one case, we group closely related species in one subgenus as taxa of the rank supraspecies, as defined above (for "aggregate of species" in the *Code*), whereas in two other cases we recognize taxa of the rank exerge (for "aggregate of subspecies" in the *Code*).

These guidelines result in taxonomic changes at low levels in three groups, the stout salamanders and two genera of modern European newts, the Alpine newts and the smooth newts.

Stout salamanders

We here elevate some former subspecies of some subgenera of the genus *Salamandra* to species level, whereas in other cases the information currently available is too scanty to do it for the time being

The North African subgenus contains at least four very different "groups of populations" (STEINFARTZ et al., 2000; DONAIRE BARROSO & BOGAERTS, 2003; ESCORIZA et al., 2006): one in eastern Algeria (including the mount Edough near Bôna, onymotope of the current subspecies *S. a. algira*), one in western Algeria and eastern Morocco (including the Beni Snassen mountains, onymotope of the current subspecies *S. algira spelaea*, and one west Algerian population currently referred to *S. a. algira*), one in the central Rif mountains and the Middle Atlas in Morocco (currently referred to *S. a. algira*), and one in the Tangitanian region in extreme northern Morocco (*S. algira tingitana*). According to STEINFARTZ et al (2000), the genetic difference between the onymotopic population of *algira*, and that of Chefchaouen in the Rif, is very high, suggesting probable specific differentiation. However, ESCORIZA & COMAS (2007) stated that the Beni Snassen population (*spelaea*) is more closely related to eastern Algerian populations than to the nearby population from the central Rif mountains. We therefore propose to recognize three distinct species, *Salamandra tingitana* (**new onymorph**) for the Tingitanian populations, *Salamandra algira* with two subspecies (*algira* and *spelaea*), and a still unnamed species in the Rif and the Middle Atlas. The species *tingitana* is easily distinguished from the other two species by its very different morphology, its viviparous mode of reproduction and its different ethology, as shown by its special requirements in captivity

The subgenus of the Near East is composed of at least four different "groups of populations" (STEINFARTZ et al., 2000), but their current assignement to the subspecies already named is still impossible due to the lack of clear delimitation of the populations and of insufficient molecular work Here we simply use the traditional subspecific taxonomy of three subspecies within a single species *infraimmaculata*, but this group requires revision

In the Alpine subgenus, on the basis of the data of STEINFARTZ et al (2000) RIBERON et al (2004), BONATO & STEINFARTZ (2005) and Veronique Helfer (personal communication), we consider *Salamandra atra* and *Salamandra aurorae* (**new onymorph**) as two distinct species, with three subspecies in the former species. In contrast with these authors, we recognize the subspecies *prenjensis* from Bosnia & Herzegovina, Serbia, Montenegro and Albania, because it is isolated from the other populations in the non-Dinaric Alps and shows morphological differences from them, being smaller and slightly different in coloration Its vulnerability fully justifies its formal taxonomic recognition.

Specific and intraspecific differentiation is high within the hyponymous subgenus *Salamandra* as here defined. Recent analyses (Steinfartz et al., 2000, García-París et al., 2003, Escoriza et al., 2006; Weisrock et al., 2006) allowed to identify several holophyletic groups in this group, which are here taxonomically recognized at different levels. We recognize three species, three exerges (aggregates of subspecies) and twelve subspecies within this taxon. The various taxa within this complex can be arranged in three major groups.

The first group, from southern Spain, includes, in our view, a good species, *Salamandra (Salamandra) longirostris* (**new onymorph**), and two subspecies of the hyponymous species. The former is an ancient isolated population considered basal to other *Salamandra* and close to the African North African salamanders, from which it is only separated by the Gibraltar strait (García-París et al., 2003). *Salamandra longirostris* (**new onymorph**) is a species of medium size, with many yellow spots. It is ovoviviparous but has a short aquatic larval period. It is striking in showing low adaptatability in captivity (personal observations, JR). The two subspecies *crespoi* and *morenica* still show intergradation with more northern subspecies of *Salamandra salamandra* (García-París et al., 2003) and thus do not deserve to be recognized as species. We include them in an exerge *crespoi* of the species *S. salamandra*.

The second group defined by Steinfartz et al. (2000) and supported by the data of Highton (2000) and García-París et al. (2003) contains two subgroups that are molecularly close to one another but more remote from the third subgroup with which they are in contact in some populations. These two subgroups are most likely remnants of an old lineage. They are very disjunctive geographically, one (*gigliolii*) being found in southern Italy, and the other one (*alfredschmidti*, *bernardezi* and *fastuosa*) in northern Spain and southwestern France. Although morphologically distinct, these taxa do not seem to be reproductively isolated from the subspecies of *S. salamandra* with which they are in contact and thus do not deserve to be recognized as distinct species. We group these four subspecies in an exerge *fastuosa* of the species *S. salamandra*.

The third and last group defined by Steinfartz et al. (2000) contains the remaining six subspecies, as well as *Salamandra (Salamandra) almanzoris* (**new onymorph**) from central Spain, which we here elevate to species level (see also García-París et al., 2003; Martínez-Solano et al., 2005). It is also considered as a relict unit with a special evolutionary history ("ESU", see above), and is currently in competition with a more modern population (*bejarae*) coming from the North. *Salamandra almanzoris* (**new onymorph**) has a small size, with a rather slender habitus and very few yellow spots. It is ovoviviparous with a long aquatic larval period, and remains very aquatic in the adult stage (Cahet, 1963). It shows low adaptability in captivity and is very different morphologically from the nearby populations of *bejarae*.

As a whole, *Salamandra (Salamandra) salamandra*, as here restricted, is a species from southern and central Europe, with a small to large size, and many yellow spots or yellow bands. It is ovoviviparous or viviparous. It shows high adaptability in captivity.

Alpine newts

The recent data of Sotiropoulos et al. (2007) suggest the existence of three well-supported different holophyletic groups in the species *Ichthyosaura alpestris*, which in our opinion should be recognized taxonomically. These are a relict group (A) represented in south-eastern Serbia, a western European group (B-C) and an eastern European group (D-E). Both these latter groups can further be divided into two groups each, respectively (B) and (C), and (D) and (E). The data of these authors do not suggest the recognition of several species, although we consider it very likely that some of the taxa discussed below will have to be raised to species level when more data are available. It is impossible at this stage to provide a complete infraspecific taxonomy of this species, because species-series nomina are lacking for some taxa that should be recognized as subspecies. SOTIROPOULOS et al. (2007, 2008) failed to describe and name the subspecies from south-eastern Serbia, from north-estern Italy and from Greece uncovered by their analysis. We just provide here brief guidelines for the taxonomy of this group.

We think that this species should be divided in at least three exerges, possibly five. It will be possible to name the first exerge only when the populations of group (A) have been formally described and named as a new subspecies, its nomen will also provide the nomen for the exerge. For the time being, we suggest to recognize only two exerges for the other two groups, but a finer analysis may require further splitting.

The western European group (B-C), the *alpestris* exerge, includes at least five groups of populations that deserve in our opinion the status of subspecies. An Italian group (B) includes the subspecies *Ichthyosaura alpestris apuana* **(new combination)** and *Ichthyosaura alpestris inexpectata* **(new combination)**. Contrary to SOTIROPOULOS et al. (2007), we maintain the latter as a valid taxon because of geographic discontinuity between this subspecies and *apuana*, of the morphological (DUBOIS & BREUIL, 1983) and genetical (BREUIL, 1983, 1986; ANDREONE, 1990) differences between them, and because its bearing a distinct Latin nomen provides support for the conservation of this very small and endangered isolate, known only from four populations (DUBOIS, 1998*b*). A northern Spanish group (C1) corresponds to the subspecies *Ichthyosaura alpestris cyreni* **(new combination)**. No nomen is clearly available for a subspecies that should be recognized for the populations of north-eastern Italy that came out as a well-supported group (C2) in the analysis of SOTIROPOULOS et al. (2007). The nomen *Triton alpestris lacusnigri* Seliškar & Pehani, 1935, and its synonym *Triton alpestris lacustris* Seliškar & Pehani, 1935, created for populations of Slovenia, might however possibly apply to this taxon. Finally, the nomen *Ichthyosaura alpestris alpestris* **(new combination)**, which has several synonyms, applies to the subspecies (C3) that straddles northern and central Europe from France to northern Romania.

Because of the Rule of Priority applying to "aggregates of subspecies", the eastern European group (D-E) must bear the nomen of *reiseri* exerge. It first includes a group (D), mostly from Greece, among which several subgroups (D1) to (D4) were clearly identified (SOTIROPOULOS et al., 2007, 2008), but for which a single nomen, *Ichthyosaura alpestris veluchiensis* **(new combination;** not "*velouchiensis*", as spelt by SOTIROPOULOS et al., 2007: 219), is currently available. Finally, the central European group (E) includes at least two subgroups. Despite morphological heterogeneity and a strong tendency to neoteny, the subgroup (E1) from Montenegro is genetically homogeneous (BREUIL & GUILLAUME, 1985; SOTIROPOULOS et al., 2007) and should better be recognized as a single subspecies, for which the nomen *Ichthyosaura alpestris montenegrina* (Radovanovic, 1951) **(new combination)** has priority. The other subgroup (E2), that straddles central Europe from Croatia to southern Romania and the Rodope mountains in Bulgaria and Greece, is possibly still heterogeneous. At this stage we propose to recognize two subspecies in this group, *Ichthyosaura alpestris reiseri* (Werner, 1902) **(new combination)** from the Prokoško lake in Bosnia & Herzegovina, and *Ichthyosaura alpestris carpathica* (Dely, 1959) **(new combination)** for the other populations. Whereas the latter populations had until now not been separated from the hyponymous subspecies, the subspecies *reiseri* has long been recognized as distinct from the latter, and the use of a distinct nomen for it could be used as an argument for its conservation. Unfortunately, this subspecies appears to be extinct, following the introduction of trouts in the lake where it lived (DUBOIS, 1998*b*). Other populations of Alpine newts can be found on the Vranica mountain where this lake occurs, but they do not have the wide head so characteristic of *reiseri* (Michel Breuil, personal communication) and seem therefore to belong in the subspecies *carpathica*.

Large European newts

The genus *Triturus*, in the current narrow acceptation of the term (for the species *cristatus*, *marmoratus* and their relatives) has been the matter of numerous hybridization studies (see a subcomplete list of references in MACGREGOR et al., 1990: 339-340). Spontaneous hybridization between *cristatus* and *marmoratus* has long been known to exist in western France, where it results in newts of phenotypes "Blasii" and "Trouessarti", but without entailing a reciprocal gene flow between the two species. Gene flow appears also to be hampered, limited or asymmetrical in several other contact zones between taxa of this group, which has resulted in the recent years in the raising of several subspecies to species rank. We support these decisions. Of particular interest and significance is the case of the two taxa *cristatus* and *carnifex*, long considered as subspecies of a single species *cristatus* but now considered distinct species. In the Geneva basin, which was inhabited by the former, the latter was introduced in recent times. Although in captivity these two forms hybridize without difficulty, in nature in this area they seldom did so, but they experienced drastic competition, and *carnifex* progressively wiped *cristatus* out of this basin (ARNTZEN & THORPE, 1999). This is a good illustration of the mayron concept and of the fact that the existence of hybrids between two taxa does not necessarily mean that they are the same taxonomic species.

European smooth newts

In parallel with the situation in *Triturus*, and following largely the guidelines of HIGHTON (2000), we here elevate several former subspecies of the genus *Lissotriton* to species level.

The situation is rather simple in the subgenus *Meinus*. According to MARTÍNEZ-SOLANO et al. (2006), a significant geographic variation exists in *L. boscai*, with two major holophyletic groups in western and central Iberian peninsula, a south-western and a central-northern one. These authors, as well as MONTORI & LLORENTE (2005) and RAFFAËLLI (2007), suggested that these two groups deserve recognition as separate species, and we implement this change here, by resurrecting the nomen *Triton maltzani* Boettger, 1879 for the south-western species. *Lissotriton maltzani* **(new combination)** can be distinguished from *L. boscai* by its smaller size (55-80 mm vs. 75-100 mm) and by its dorsal coloration, which is paler than in *boscai*, especially in females, with less distinct dark spots.

The situation is more complex in the subgenus *Lissotriton*.

In the species *Lissotriton helveticus*, we here recognize the subspecies *alonsoi* and *punctillatus* following GARCÍA-PARÍS et al. (2004).

In the species *Lissotriton italicus*, RAGGHIANTI et al. (1980) showed the existence of a chromosomal polymorphism distinguishing the northern and southern populations. RAGGHIANTI & WAKE (1986) found allozyme polymorphism in the species but their data did not support specific status for the two groups (see also HIGHTON, 2000: 228). As the chromosomal differentiation between the two groups appears clear, we recognize them as subspecies. The nomen *Lissotriton italicus italicus* (Peracca, 1898) **(new onymorph)** applies to the southern subspecies and we propose to revalidate the nomen *Molge italica molisana* Altobello, 1926 for the northern one, as *Lissotriton italicus molisanus* **(new combination)**. According to LANZA (1977), the series of symphoronts of this taxon was heterogeneous, being composed in part of *Lissotriton italicus* and of *Lissotriton meridionalis* specimens. As these specimens appear to have been lost, final stabilization of the status of this nomen will require the designation and description as neophoront of a *L. italicus* specimen from the Campobasso region (Molise, Italy).

The supraspecies *vulgaris* poses a difficult problem. RAXWORTHY (1990) recognized two species, *Lissotriton montandoni* and *Lissotriton vulgaris*, and reviewed the infraspecific taxonomy of the latter, with seven subspecies, known to hybridize in nature with each other and also with *montandoni*. He stated that "*there can be no question of raising these taxonomic units to species rank based on the biological species concept*" (p. 491). Recently however, BABIK et al. (2005) produced an interesting detailed phylogeographic analysis of this group, which in our opinion should entail taxonomic changes. They showed that the species *montandoni* was cladistically nested within the *vulgaris* group, rendering it paraphyletic. Several subgroups of *montandoni*, with different mitochondrial genomes, were uncovered by this analysis. It is likely that in some at least of these groups, several events of partial introgression of *vulgaris* mitochondrial genome took place in the last million years. Although important in some cases, the introgression of *vulgaris* mitochondrial alleles in *montandoni* does not seem to have significantly altered the morphology and ethology of the latter, which remains very homogeneous morphologically, in behaviour and habits throughout its range (JR, personal observations). The two species are readily distinguished in morphology and morphometrics, allozymes, chromosomes and courtship behaviour (see list of references in BABIK et al., 2005: 2488). Both species show a marked, although incomplete, behavioural sexual isolation (MICHALAK et al., 1998; MICHALAK & RAFIŃSKI, 1999). Therefore, just like in some populations of *Salamandra* mentioned above, *montandoni* and *vulgaris* clearly behave as separate entities in the field and should be recognized taxonomically as distinct mayrons. This is an example of the genetic homeostasy that characterizes mayrons, a fact that was stressed e.g. by MAYR (1975) with his concept of "cohesion of the genotype" and by TEMPLETON (1989) with his "cohesion species concept". To put the things shortly and schematically, it appears that *montandoni* populations have "accepted" local and limited genetic introgressions from *vulgaris*, as far as these genetic changes did not significantly alter their overall phenotype and biology, i.e., as long as they allowed them to "remain *montandoni*".

The recognition of *montandoni* as a species distinct from *vulgaris* makes the latter paraphyletic and requires its splitting into several species. This is further justified by the existence of clear morphological differences between them and by the fact that gene flow between them, where they meet, appears hampered and incomplete, with exchanges of portions of genomes which however do not obscure the recognition of the different entities (Babik et al., 2005). This taxonomic decision is similar to what has been done recently in the genus *Triturus* (see above). On the basis of the data of Babik et al. (2005), we suggest that the following six species should be recognized in this supraspecies: *Lissotriton graecus* (Wolterstorff, 1905) **(new combination)**, *Lissotriton kosswigi* (Freytag, 1955) **(new combination)**, *Lissotriton lantzi* (Wolterstorff, 1914) **(new combination)**, *Lissotriton meridionalis* (Boulenger, 1882) **(new combination)**, *Lissotriton montandoni* (Boulenger, 1880) and *Lissotriton vulgaris* (Linnaeus, 1758). We provide below taxognoses for these species. Additionally, we recognize a subspecies *Lissotriton vulgaris ampelensis* (Fuhn, 1951) **(new combination)** in the species *vulgaris* (see Rafiński et al., 2001; Iftime & Iftime, 2008). One of these nomina, *lantzi*, was first published (Wolterstorff, 1914) as a quadrinomen (for a taxon below the rank subspecies) and was therefore unavailable in this original publication. Following a request by Mertens & Wermuth (1960*a*), this nomen was validated by the ICZN (Riley & China, 1962), a strange decision indeed, as this nomen had already been made available by Nikolsky (1918: 231), who had used it as a trinominal (*Molge vulgaris lantzi*) and had provided a diagnosis and a description. The nomen *ampelensis* was credited by Mertens & Wermuth (1960*b*: 32) to Fuhn & Freytag (1952), as a quadrinominal, but it was first used by Fuhn (1951) as a trinominal, with a description, and is therefore available with this author and date.

Raxworthy (1990) recognized a subspecies *dalmaticus* (Kolombatović, 1907) which we consider as a synonym of *vulgaris* (see Krizmanić et al., 1997; Babik et al., 2005). Several recent authors (e.g., Raxworthy, 1990, Babik et al., 2005) recognized a subspecies *schmidtlerorum*, which we also consider as a synonym of *vulgaris* (see Olgun et al., 1999, Thorn & Raffaëlli, 2001; Raffaëlli, 2007). Anyway, if it was to be recognized as a valid taxon, this should be under its original spelling *schmidtleri* (Raxworthy, 1988). For reasons explained by Dubois (2007*b*), the spelling *schmidtlerorum* is an invalid but available emendation that should be credited to Raxworthy (1990, 482). Finally, as for the nomen *tomasinii* Wolterstorff, 1908, used by Krizmanić et al. (1997) and Ćirović et al. (2008) for a subspecies of *vulgaris*, this nomen is nomenclaturally unavailable, having been published as a quadrinomen and never validated by subsequent authors, and its validity is not supported by recent molecular and morphological studies (Spartak Litvinchuk, personal communication). If these populations from Montenegro had to be recognized as a subspecies of *graecus*, this would require the publication of a description and a nomen for them, as for the time being no available nomen exists for this taxon.

New, resurrected and emended taxa, nucleospecies designations and nomenclatural comments

In this work, we strictly respect the rules of the *Code* regarding the number of ranks that can be used in zoological taxonomy. Therefore, as explained above, we only use two ranks in the genus-series (genus and subgenus) and four in the species-series (supraspecies, species, exerge and subspecies). In the family-series, although the *Code* allows for an undetermined number of ranks below family, for the purpose of our ergotaxonomy of the *Salamandridae* we only need the following four ranks: subfamily (nomen ending in *-INAE*), tribe (*-INI*), subtribe (*-INA*) and infratribe (*-ITA*).

For several of the new subgenera that we propose to recognize here, nomina are already available or can be made available through appropriate designation of nucleospecies. In order to clarify and stabilize their place in synonymies, we also designate below nucleospecies for all the nominal genera of *SALAMANDRIDAE* for which this had not been done previously, and we provide a few additional nomenclatural comments.

For each of the unnamed taxa that we first recognize here, we provide below a new nomen with its etymology and grammatical gender. To avoid the creation of long nomina like *Lyciasalamandra* or *Paramesotriton*, we use below the following simple roots for nomina designating some new taxa "*-triton*", from the generic nomen *Triton* Laurenti, 1768 (from the Greek *Triton*, son of Poseidon and God of the sea), for genera of "newts"; and "*-andra*", the last five letters of the nomen *Salamandra* Laurenti, 1768 (from the Greek *salamandra*, "salamander"), for genera of "true salamanders". Other roots used in a few other cases are explained where appropriate.

In the section below we only discuss the family-series and genus-series taxa that are created or modified (emended) here, but not those which are used here in the same sense and with the same content as in the recent literature, nor those of the species-series, for which we provide no new nomen. Taxa are presented below by alphabetical order of their nomina at all levels. We do not provide in the text below the lists of the species included in each of the new or emended taxa defined below, as they appear in the complete new ergotaxonomy of the family *SALAMANDRIDAE* Goldfuss, 1820 which is given in table 5.

For each taxon discussed below, we provide short definitions or taxognoses, in the forms of an *entexognosis*, a *diagnosis* (in one of the tables 1-4) and an *idiognosis* (see above for explanations).

The entexognoses provide phylogenetic definitions of the taxa as holophyletic groups including and excluding a few chosen species.

The characters used in the diagnoses were described in TWITTY (1964), MECHAM (1967*a-b*, 1968), SALTHE (1967), THORN (1969), MORESCALCHI (1975), NUSSBAUM & BRODIE (1981*a-c*), PECIO & RAFINSKI (1985), TITUS & LARSON (1995), SPARREBOOM et al. (2000), CHAN et al. (2001), FEI et al. (2006), WEISROCK et al. (2006) and RAFFAËLLI (2007). We also use some of the characters provided in the original descriptions of some taxa, as well as personal observations and those of several colleagues and friends (see *Acknowledgements*).

Size in the diagnoses is given as TL (total length in millimetres, from tip of snout to tip of tail). For the purpose of these diagnoses, we recognize four different breeding behaviours in the *SALAMANDRIDAE* (SALTHE, 1967; TITUS & LARSON, 1995): nuptial dance, type I amplexus or "caudal capture", type II amplexus or "ventral capture", type III amplexus or "dorsal capture". Two distinct modes of nuptial dance can also be distinguished: a "simple" one in which the male and female follow each other, and an "elaborated" one, in which the male executes caudal movements. Three kinds of reproduction modes exist in the genus *Salamandra*, which, according to the terminology of DUBOIS (2004*b*) are here designated as follows: *ovoviviparity lecithotroph*, for embryos developing within the eggs kept in the female genital tract, feeding on the vitelline reserves of the eggs, *viviparity adelphotroph* for embryos that develop within the female genital tract, feeding on their brothers and sisters; and *viviparity matrotroph* for embryos that develop within the female genital tract, feeding on secretions of the latter. Another, rather unusual, character, that we use in taxognoses, is the adaptability of the species to terrarium, for which, based on the personal experiences of one of us (JR) and of several other breeders (personal communications), we recognize two categories: *high adaptability in terrarium* (HAT), for species that can be kept for several years in captivity under various conditions of temperature, humidity and food offer, in terraria where they can develop complete breeding behaviour and give birth to offspring, sometimes repeatedly, and *low adaptability in terrarium* (LAT), for species that do not easily reproduce in captivity and are reluctant to variability for conditions of temperature, humidity, food offer and general husbandry; in the last case, animals must be kept under strict conditions of captivity which have to be determined on a permanent basis. This criterion expresses in a synthetic way several ethological, physiological and more generally biological characteristics and limitations of the organisms (requirements and constraints regarding temperature, humidity, space, shelter, etc.), that have not been analysed in detail yet although this would certainly be possible.

Beside entexognoses and diagnoses, we provide short idiognoses for most of the taxa, which give a few major characters in a non-comparative way. All these idiognoses follow the same plan: (1) Size (range or maximum known for each taxon). (2) Morphology. (3) Coloration. (4) Sex dimorphism. (5) Behaviour. (6) Adaptability in terrarium. (7) Distribution. (8) Miscellanea.

The higher nomenclature of the Urodela used below is that of Dubois (2005*c*). If a class-series taxon, e.g. of rank phalanx (see Dubois, 2006*a*) is to be recognized for the group including the families *Ambystomatidae* and *Salamandridae*, its valid nomen is **Mutabilia** Merrem, 1820, a senior synonym of **Treptobranchia** Frost et al., 2006 (see Dubois & Ohler, 2009).

Classis **Amphibia** De Blainville, 1816

Subclassis **Neobatrachi** Sarasin & Sarasin, 1890

Superordo **Batrachia** Brongniart, 1800

Ordo **Urodela** Dumeril, 1806

Phalanx **Mutabilia** Merrem, 1820

Family ***Salamandridae*** Goldfuss, 1820

Subfamilia ***Pleurodelinae*** Tschudi, 1838

Nucleogenus. – *Pleurodeles* Michahelles, 1830: 195, by implicit etymological designation.

Entexognosis. – The most inclusive holophyletic taxon including the species *Pleurodeles waltl* (Michahelles, 1830) and excluding the species *Salamandra salamandra* (Linnaeus, 1758) and *Salamandrina perspicillata* (Savi, 1821).

Diagnosis. – See table 1.

Table 1. – Diagnostic comparisons among five groups composed of three parordinate taxa as recognized here.

Superordinate taxon	**Familia *SALAMANDRIDAE* Goldfuss, 1820**		
Parordinate taxa	**Subfamilia *PLEURODELINAE* Tschudi, 1838**	**Subfamilia *SALAMANDRINAE* Goldfuss, 1820**	**Subfamilia *SALAMANDRININAE* Fitzinger, 1843**
Frontosquamosal arch	Present	Absent	Present
Premaxillary bones	Paired or fused	Paired	Paired
Diploid chromosome number	24 or 22	24	24
Dorsal lordose	Present	Absent	Present
Breeding behaviour	Nuptial dance (simple or elaborated), or type I, II or III amplexus	Type II amplexus	Nuptial dance (simple)
Superordinate taxon	**Subtribus *MOLGINA* Gray, 1850**		
Parordinate taxa	**Infratribus *CYNOPITA* nov**	**Infratribus *EUPROCTITA* nov**	**Infratribus *MOLGITA* Gray, 1850**
Skull	Boxlike, with flattened dorsal surface	Very flattened	Not flattened (except in *Calotriton*); narrow, sometimes boxlike
Frontosquamosal arch	Complete	Nearly absent	Absent, incomplete or complete
Lungs	Present	Absent or very reduced	Present
Ventral coloration	Always red or reddish	Never red or reddish	Never fully red
Breeding behaviour	Nuptial dance (elaborated)	Type I amplexus	Type I amplexus or nuptial dance (elaborated)
Adaptability in terrarium	HAT or LAT	LAT	HAT
Superordinate taxon	**Subgenus *Lissotriton (Lissotriton)* Bell, 1839**		
Parordinate taxa	**Supraspecies *helveticus* (Razoumowsky, 1789)**	**Supraspecies *italicus* (Peracca, 1898)**	**Supraspecies *vulgaris* (Linnaeus, 1758)**
Size	TL 65-92 mm	TL 55-80 mm	TL 70-111 mm
Dorsal crest in breeding male	Present	Absent	Present
Palm on toes in breeding male	Present	Absent	Present
Tail fin in breeding male	Present	Present	Present or absent
Spots on venter of male	Absent	Present	Present or absent
Horizontal black line through eye	Present	Absent	Present
Whip during male nuptial dance	Well-developed	Attenuated	Well-developed
Adaptability in terrarium	HAT	LAT	HAT or LAT
Superordinate taxon	**Subgenus *Salamandra (Salamandra)* Laurenti, 1768**		
Parordinate taxa	**Species *Salamandra almanzoris* Muller & Hellmich, 1935**	**Species *Salamandra longirostris* Joger & Steinfartz, 1994**	**Species *Salamandra salamandra* (Linnaeus, 1758)**
Size	TL up to 130 mm	TL up to [illegible]88 mm	TL [illegible]10-280 mm
Habitus	Slender	Stout	Slender to stout
Head	Small, narrow	Medium, rather wide	Small to large, narrow to wide
Snout	Pointed	Very pointed	Rounded to pointed
Yellow spots or bands	Very few spots	Many large spots	Spots or bands
Red (or orange) colour	Absent	Absent	Present
Reproduction mode	Ovoviviparity lecithotroph	Ovoviviparity lecithotroph	Ovoviviparity lecithotroph or viviparity adelphotroph
Duration of free larval development	Long	Short	Short to long, or absent
Altitudinal distribution	High	Medium	Low to high
Adaptability in terrarium	LAT	LAT	LAT to HAT
Superordinate taxon	**Species *Salamandra salamandra* (Linnaeus, 1758)**		
Parordinate taxa	**Exerge *crespoi* Malkmus, 1983**	**Exerge *fastuosa* Schreiber, 1912**	**Exerge *salamandra* (Linnaeus, 1758)**
Size	TL up to 280 mm	TL [illegible]10-160 mm	TL 200-280 mm
Habitus	Stout	Slender	Stout
Head	Narrow	Narrow	Wide
Spots or lines	Spots	Lines	Lines or spots
Yellow colour	Not extensive	Extensive	Rarely extensive
Red colour	Always	Rare	Rare
Orange colour	Never	Never	Rare
Reproduction mode	Ovoviviparity lecithotroph	Viviparity adelphotroph (ovoviviparity lecithotroph in *gigliolii*)	Ovoviviparity lecithotroph
Adaptability in terrarium	LAT	HAT	LAT

Tribus *Molgini* Gray, 1950

Nucleogenus. – *Molge* Merrem, 1820: 166, by original specific monophory.

Entexognosis. – The most inclusive holophyletic taxon including the species *Pleurodeles waltl* (Michahelles, 1830) and excluding the species *Triturus cristatus* (Laurenti, 1768).

Diagnosis. – See table 2.

Subtribus *Molgina* Gray, 1950

Nucleogenus. – *Molge* Merrem, 1820: 166, by implicit etymological designation.

Entexognosis. – The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Taricha torosa* (Rathke, 1833).

Diagnosis. – See table 2.

Idiognosis. – (1) TL 55-250 mm. (2) Habitus slender to stout. (3) Dorsal and ventral colorations usually very contrasted. (4) Sex dimorphism strong. Dorsal crest present or absent. (5) Breeding habitat lentic or lotic. Type I amplexus or nuptial dance (elaborated). (6) HAT or LAT. (7) Palearctic.

Infratribus *Cynopita* nov.

Nucleogenus. – *Cynops* Tschudi, 1838: 59, by present designation.

Entexognosis. – The most inclusive holophyletic taxon including the species *Cynops pyrrhogaster* (Boie, 1826) and excluding the species *Euproctus platycephalus* (Gravenhorst, 1829) and *Triturus cristatus* (Laurenti, 1768).

Diagnosis. – See table 1.

Idiognosis. – (1) TL 70-250 mm. (2) Habitus usually stout. Head boxlike. Trunk usually quadrangular. Skin smooth to very granular. (3) Dorsal coloration usually dull. Ventral coloration bright, with red, reddish or orange spots. (4) Sex dimorphism strong. (5) Mainly aquatic, in lentic or lotic habitat. Nuptial dance (elaborated). (6) HAT or LAT. (7) Eastern Palearctic and northern Oriental regions. (8) Distal tarsal 4 and 5 fused.

Genus **Cynops** Tschudi, 1838

Nucleospecies. – *Salamandra subcristata* Temminck and Schlegel, 1838: 117 (neonym for *Molge pyrrhogaster* Boie, 1826: 215), by original specific monophory.

Etymology. – From the Greek *kunos*, genitive of *kuon* ("dog") and *opsis* ("aspect, appearance"). This nomen clearly refers to the fact that the head of males of *Cynops pyrrhogaster*, the species used for the description of the genus, looks like a dog's head, because of its very sharp canthus rostralis and of the presence of an excrescence at the rear of the head. These two characters however are absent in *ensicauda*, the other species of this genus.

Grammatical gender. – Masculine.

Entexognosis. The most inclusive holophyletic taxon including the species *Cynops pyrrhogaster* (Boie, 1826) and excluding the species *Hypselotriton wolterstorffi* (Boulenger, 1905), *Pachytriton brevipes* (Sauvage, 1877), *Laotriton laoensis* (Stuart & Papenfuss, 2002) (**new combination**) and *Paramesotriton deloustali* (Bourret, 1934).

Diagnosis. – See table 3.

Idiognosis. (1) Medium (TL 120-150 mm). (2) Habitus stout Trunk quadrangular Skin very granular. (3) Dorsal coloration usually dull Ventral coloration very bright, with red, reddish or orange spots. (4) Sex dimorphism strong, male smaller than female. (5) Mainly aquatic, in lentic habitat. (6) HAT (7) Japan (8) Nasals broadly in contact, sharp vertebral ridge.

Genus **Hypselotriton** Wolterstorff, 1934

Nucleospecies. *Molge wolterstorffi* Boulenger, 1905. 277, by original designation

Etymology. From the Greek *hupselos* ("high") and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Hypselotriton wolterstorffi* (Boulenger, 1905) and excluding the species *Cynops pyrrhogaster* (Boie, 1826), *Pachytriton brevipes* (Sauvage, 1877), *Laotriton laoensis* (Stuart & Papenfuss, 2002) and *Paramesotriton deloustali* (Bourret, 1934).

Diagnosis – See table 3

Idiognosis. (1) TL 70-160 mm. (2) Habitus stout. Trunk almost quadrangular. Skin smooth or slightly granular. (3) Dorsal coloration dull Ventral coloration very bright, with red, reddish or orange spots. (4) Sex dimorphism strong, male very small. (5) Mainly aquatic, in lentic habitat (6) HAT or LAT (7) China (8) Nasals separated or in slight contact; weak vertebral ridge.

Subgenus **Hypselotriton** Wolterstorff, 1934

Nucleospecies, etymology and grammatical gender See above under genus *Hypselotriton*

Entexognosis. The most inclusive holophyletic taxon including the species *Hypselotriton wolterstorffi* (Boulenger, 1905) and excluding the species *Hypselotriton granulosus* (Chang, 1933)

Diagnosis – See table 2

Idiognosis. (1) TL 70-160 mm. (2) Habitus stout. Trunk almost quadrangular. Parotoids weakly developed. Skin smooth. (3) Dorsal coloration mostly dull Ventral coloration very

Table 2. – Diagnostic comparisons among thirteen groups composed of two parordinate taxa as recognized here.

Superordinate taxon	**Subfamilia *PLEURODELINAE* Tschudi, 1838**	
Parordinate taxa	**Tribus *MOLGINI* Gray, 1850**	**Tribus *PLEURODELINI* Tschudi, 1838**
Premaxillary bones	Fused	Paired
Skin	Smooth or slightly granular	Very granular
Breeding behaviour	Type I or type III amplexus, or nuptial dance (elaborated)	Nuptial dance (simple) or type II amplexus
Superordinate taxon	**Tribus *MOLGINI* Gray, 1850**	
Parordinate taxa	**Subtribus *MOLGINA* Gray, 1850**	**Subtribus *TARICHINA* nov.**
Diploid chromosome number	24	22
Dorsal crest in breeding male	Present or absent	Absent
Breeding behaviour	Nuptial dance (elaborated) or type I amplexus	Type III amplexus
Adaptability in terrarium	HAT or LAT	HAT
Superordinate taxon	**Genus *Hypselotriton* Wolterstorff, 1934**	
Parordinate taxa	**Subgenus *Hypselotriton* Wolterstorff, 1934**	**Subgenus *Pingia* Chang, 1935**
Frontal process of premaxillary	Long	Short
Parotoid glands	Weakly developed	Well developed
Tubercules on external side of hands and feet	Present	Absent
Skin	Very slightly granular, nearly smooth	Slightly to very granular
Adaptability in terrarium	LAT	HAT or unknown
Altitudinal distribution	High altitude (1800-2600 m)	Low altitude (0-1000 m)
Superordinate taxon	**Genus *Paramesotriton* Chang, 1935**	
Parordinate taxa	**Subgenus *Allomesotriton* Freytag, 1983**	**Subgenus *Paramesotriton* Chang, 1935**
Habitus	Slender	Robust
Skull	Long and narrow	Short and broad
Frontosquamosal	Incomplete	Complete
Epibranchials	Moderately stout and bony	Very stout and bony
Dorsal coloration	Clear	Dark
Habitat	Very aquatic, flowing water	Slightly aquatic, mildly flowing water
Superordinate taxon	**Genus *Lissotriton* Bell, 1839**	
Parordinate taxa	**Subgenus *Lissotriton* Bell, 1839**	**Subgenus *Meinus* nov.**
Frontosquamosal arch	Weak, sometimes entirely ligamentary	Very strong
Female cloaca	Slightly turgescent but not prominent	Cone-shaped, very prominent
Whip and wave during male nuptial dance	Present (reduced in *L. italicus*)	Absent
Habitat	Mainly terrestrial, aquatic only during breeding	Very aquatic
Adaptability in terrarium	HAT	LAT
Superordinate taxon	**Genus *Neurergus* Cope, 1862**	
Parordinate taxa	**Subgenus *Musergus* nov.**	**Subgenus *Neurergus* Cope, 1862**
Ventral coloration	Dark, with median longitudinal orange band	Bright
Colour on sides of tail of breeding male	Silver-blue	Not silver-blue
Superordinate taxon	**Genus *Triturus* Rafinesque, 1815**	
Parordinate taxa	**Subgenus *Pyronicia* Gray, 1858**	**Subgenus *Triturus* Rafinesque, 1815**
Dorsal coloration	Green	Black
Ventral coloration	Black and white	Yellow or orange with black spots
Dorsal crest of breeding male	Undulating	Denticulated
Habitat	Highly terrestrial	Rather aquatic
Adaptability in terrarium	LAT	HAT
Superordinate taxon	**Genus *Notophthalmus* Rafinesque, 1820**	
Parordinate taxa	**Subgenus *Notophthalmus* Rafinesque, 1820**	**Subgenus *Rafinus* nov.**
Spots on dorsum and venter	Small	Large
Male secondary sex character	Transverse black horny ridges on thighs	No transverse black horny ridges on thighs
Eft stage	Present	Absent
Neoteny	Present	Absent
Habitat	Very aquatic	Mainly terrestrial, aquatic only during breeding period

Table 2 (continued).

Superordinate taxon	**Genus *Tancha* Gray, 1850**	
Parordinate taxa	**Subgenus *Tancha* Gray, 1850**	**Subgenus *Twittya* nov.**
Iris	Yellow or partially yellow	Black
Ventral coloration	Yellow to orange	Red
Egg deposition	Singly or in clumps of 7-39 eggs	Clumps of 6-16 eggs
Habitat	Standing or mildly flowing water	Flowing water
Superordinate taxon	**Genus *Tylototriton* Anderson, 1871**	
Parordinate taxa	**Subgenus *Tylototriton* Anderson, 1871**	**Subgenus *Yaotriton* nov.**
Size	TL up to 230 mm	TL 120-160 mm
Dorsal coloration	Black with colored spots	Mainly black
Deposition site of eggs	In water	On land or in contact with water
Habitat	Partially aquatic	Terrestrial
Adaptability in terrarium	HAT	LAT
Superordinate taxon	**Subfamilia *SALAMANDRINAE* Goldfuss, 1820**	
Parordinate taxa	**Tribus *CHIOGLOSSINI* nov.**	**Tribus *SALAMANDRINI* Goldfuss, 1820**
Size	TL 150-200 mm	TL 110-324 mm
Habitus	Slender	Stout
Premaxillaries	Paired with short posterior prolongations	Paired with long posterior prolongations
Nasals	Large, in contact with each other	Small, separated from each other
Reproduction mode	Oviparity	Ovoviviparity or viviparity
Mode of life	Mainly aquatic	Terrestrial
Adaptability in terrarium	LAT	HAT
Superordinate taxon	**Subgenus *Algiandra* nov.**	
Parordinate taxa	**Species *Salamandra algira* Bedriaga, 1883**	**Species *Salamandra tingitana* Donaire Barroso & Bogaerts, 2003**
Size	TL up to 230 mm	TL up to 210 mm
Habitus	Slender	Stout
Glands on dorsum of breeding male	Absent	Present
Yellow spots	Small spots, often regular	Very small spots, irregular sometimes absent
Red colour	Present	Absent
Reproduction mode	Ovoviviparity lecithotroph	Viviparity adelphotroph
Adaptability in terrarium	LAT	HAT
Superordinate taxon	**Subgenus *Alpandra* nov.**	
Parordinate taxa	**Species *Salamandra atra* Laurenti, 1768**	**Species *Salamandra aurorae* Trevisan, 1982**
Head	Narrow	Moderately narrow
Dorsal coloration	Black, sometimes very few yellow spots	Black yellow bands
Distribution range	Large	Narrow
Adaptability in terrarium	LAT	HAT

bright, red (4) Sex dimorphism strong, male very small. (5) Fully aquatic, in lentic habitat. (6) LAT, with a narrow gradient of temperature (12-25°C). (7) Western China (8) Tubercules on the external side of hands and feet.

Subgenus **Pingia** Chang, 1935

Nucleospecies. *Pachytriton granulosus* Chang, 1933, 320, by original specific monophory

Etymology From the patronym of Prof. Chih Ping (1886-1965), then director of the biological laboratory of Nankin (CHANG, 1936, 3, 103).

Grammatical gender. Feminine

Entexognosis - The most inclusive holophyletic taxon including the species *Hypselotriton granulosus* (Chang, 1933) and excluding the species *Hypselotriton wolterstorffi* (Boulenger, 1905).

Table 3 Diagnostic comparisons among a group composed of five parordinate taxa as recognized here

Superordinate taxon	Infratribus *CYNOPITA* nov.				
Parordinate taxa	**Genus *Cynops* Tschudi, 1838**	**Genus *Hypselotriton* Wolterstorff, 1934**	**Genus *Laotriton* nov.**	**Genus *Pachytriton* Boulenger, 1878**	**Genus *Paramesotriton* Chang, 1935**
Size	TL 120- 50 mm	TL 80- 60 mm	TL 180-250 mm	TL 160-200 mm	TL 130-200 mm
Skull	Long and thin	Thin and flat	Long, wide and flat	Wide and flat	Long and wide
Number of vertebrae	13	13	12	12-(13)	(11)-12
Parotoids	Very prominent	Slightly prominent	Very prominent	Prominent	Prominent
Tongue pad	Long	Long	Reduced, without free posterior margin	Reduced	Long
Skin	Very granular without distinct warts	Smooth to very granular without distinct warts	Very granular with distinct warts	Smooth	Usually very granular with distinct warts
Vertebral ridge	Prominent	Almost absent	Prominent	Absent	Prominent
Lateral ridges	Absent	Absent	Present	Absent	Present
Dorsal coloration	Usually dull	Dull	Bright	Dull	Dull
Adaptability in terrarium	HAT	HAT or LAT	LAT	LAT	LAT

Diagnosis. – See table 2.

Idiognosis. (1) TL 70-100 mm. (2) Habitus stout. Trunk almost quadrangular. Parotoids well developed. Skin slightly to very granular. (3) Dorsal coloration dull. Ventral coloration very bright, red. (4) Sex dimorphism strong, male small. (5) Mainly aquatic, in lentic habitat. (6) HAT, with tolerance of a large gradient of temperature (5-25°C); adaptability in captivity of *Hypselotriton granulosus* unknown. (7) Eastern China. (8) No tubercules on the external side of hands and feet.

Genus **Laotriton** nov.

Nucleospecies. *Paramesotriton laoensis* Stuart & Papenfuss, 2002: 145, by present designation.

Etymology. From the Laotian *Laos* (name of the country) and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entexognosis. The most inclusive holophyletic taxon including the species *Laotriton laoensis* (Stuart & Papenfuss, 2002) and excluding the species *Cynops pyrrhogaster* (Boie, 1826), *Hypselotriton wolterstorffi* (Boulenger, 1905), *Pachytriton brevipes* (Sauvage, 1876) and *Paramesotriton deloustali* (Bourret, 1934).

Diagnosis. – See table 3.

Idiognosis. (1) TL 180-250 mm. (2) Habitus very stout. Snout truncated, head large and very flat. Tail of female long. Skin warty, with many tubercules on upper side of trunk. (3) Dorsal and ventral coloration bright. (4) Sex dimorphism moderate. (5) Completely aquatic, in lotic habitat. (6) LAT, with tolerance of a narrow gradient of temperature (16-25°C). (7) Laos.

Genus **Paramesotriton** Chang, 1935

Nucleospecies. – *Mesotriton deloustali* Bourret, 1934: 83, by original specific monophory under *Mesotriton* Bourret, 1934: 83 (nec *Mesotriton* Bolkay, 1927: 64).

Etymology. – From the Greek *para* ("near, beside"), *mesos* ("in the middle of") and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Paramesotriton deloustali* (Bourret, 1934) and excluding the species *Cynops pyrrhogaster* (Boie, 1826), *Hypselotriton wolterstorffi* (Boulenger, 1905), *Laotriton laoensis* (Stuart & Papenfuss, 2002) and *Pachytriton brevipes* (Sauvage, 1876).

Diagnosis. – See table 3.

Idiognosis. – (1) TL 130-200 mm. (2) Habitus slender to very stout. Snout truncated, head narrow to large. Tail of female medium. Skin smooth to warty. (3) Dorsal coloration usually dull, ventral coloration bright. (4) Sex dimorphism usually moderate. (5) Usually aquatic, in lotic habitat. (6) LAT, with tolerance of a rather large gradient of temperature (10-25°C). (7) China, Vietnam.

Subgenus **Allomesotriton** Freytag, 1983

Nucleospecies. – *Trituroides caudopunctatus* Liu & Hu *in* Hu, Djao & Liu, 1973: 151, by original designation.

Etymology. – From the Greek *allos* ("different, strange"), *mesos* ("in the middle of") and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Paramesotriton caudopunctatus* (Liu & Hu *in* Hu, Djao & Liu, 1973) and excluding the species *Paramesotriton deloustali* (Bourret, 1934).

Diagnosis. – See table 2.

Idiognosis. – (1) TL 150 mm. (2) Habitus slender. Snout truncated, head narrow. Skin nearly smooth. (3) Dorsal coloration light brown, ventral coloration bright. (4) Sex dimorphism rather strong. (5) Fully aquatic, in lotic habitat. (6) LAT, with tolerance of a narrow gradient of temperature (10-20°C). (7) Southern China.

Subgenus **Paramesotriton** Chang, 1935

Nucleospecies, etymology and grammatical gender. – See above under genus *Paramesotriton*.

Entexognosis. – The most inclusive holophyletic taxon including the species *Paramesotriton deloustali* (Bourret, 1934) and excluding the species *Paramesotriton caudopunctatus* (Liu & Hu *in* Hu, Djao & Liu, 1973).

Diagnosis. – See table 2.

Idiognosis (1) TL 130-200 mm. (2) Habitus very stout. Snout truncated, head large. Skin warty, with many tubercules on upper side of trunk (3) Dorsal coloration dull, ventral coloration bright. (4) Sex dimorphism moderate. (5) Usually aquatic, in lotic habitat (6) LAT, with tolerance of a rather large gradient of temperature (10-25°C) (7) China, Vietnam.

Infratribus *Euproctita* nov

Nucleogenus *Euproctus* Gene, 1839 281, by present designation

Entexognosis. – The most inclusive holophyletic taxon including the species *Euproctus platycephalus* (Gravenhorst, 1829) and excluding the species *Cynops pyrrhogaster* (Boie, 1826) and *Triturus cristatus* (Laurenti, 1768).

Diagnosis. – See table 1.

Idiognosis. – (1) TL 130-140 mm. (2) Habitus slender Head and trunk flattened. Skin smooth. (3) Dorsal coloration usually dull Ventral coloration never red or orange (4) Sex dimorphism moderate, spur on the male hind limbs. (5) Mainly aquatic, in lotic habitat Type I amplexus. Parental care in one of two species. (6) LAT, with tolerance of a narrow gradient of temperature (5-15°C). (7) Western Palearctic (Corsica, Sardinia)

Infratribus *Molgita* Gray, 1950

Nucleogenus. *Molge* Merrem, 1820 166, by implicit etymological designation

Entexognosis - The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Cynops pyrrhogaster* (Boie, 1826) and *Euproctus platycephalus* (Gravenhorst, 1829).

Diagnosis – See table 1.

Idiognosis. (1) TL 55-180 mm (2) Habitus usually stout Head usually long and slender. Trunk rounded or slightly flattened Skin smooth or slightly granular (3) Dorsal and ventral coloration usually bright Ventral coloration rarely red or orange. (4) Sex dimorphism strong. (5) Aquatic during breeding period, in lentic or lotic habitat No amplexus, except in *Calotriton*. (6) Usually HAT. (7) Western Palearctic.

Genus **Ichthyosaura** Sonnini & Latreille, 1801

Nucleospecies. - *Proteus tritonius* Laurenti, 1768: 37, by original specific monophory

Comment As rightly pointed out by Schmidtler (2004 22), and acknowledged by Speybroeck & Crochet (2007), Lescure (2008) and Bour et al (2008), the nomen *Ichthyosaura* Sonnini & Latreille, 1801 is the first available one for the genus including the nominal species *Triton alpestris* Laurenti, 1768, and it has priority over *Mesotriton* Bolkay, 1927 (nucleospecies, *Triton alpestris* Laurenti, 1768, by subsequent designation of Thorn, 1969 191) The synonymy between the nominal species *Proteus tritonius* Laurenti, 1768 and *Triton alpestris* Laurenti, 1768 is beyond doubt, not only because the description and figure of the former fully fits a larva of newt, not of salamander, but also because both are based on specimens from the same onymotope, a small lake north-east of the top of the mount Ötscher (1893 m) in Niederösterreich (Lower Austria). A larva of *alpestris* from this locality should be designated as neotype for the specific nomen *tritonius* to stabilize definitively the status of the latter. Another newt species could possibly occur in this locality, *Lissotriton vulgaris*, but this would have to be demonstrated by new field data. No specimen of newt from this mountain is to be found in the national collections of the Naturhistorisches Museum Wien (Heinz Grillitsch, personal communication). If a larva of *vulgaris* was designated as neotype of *tritonius*, *Ichthyosaura* would have to replace *Lissotriton* as the valid nomen for the genus of smooth newts.

The nomen *Ichthyosaura* should be credited to SONNINI & LATREILLE (1801*b*), not to "Latreille *in* SONNINI & LATREILLE (1801*b*)". In the introduction of the first volume of this 4-volume work, SONNINI & LATREILLE (1801*a*) stated that Latreille had written the parts dealing with the tortoises, lizards, frogs, toads, tree-frogs and snakes, whereas Sonnini had written the part dealing with the salamanders and the introduction. But they did not state who had written the part entitled "Eclaircissemens [sic] et additions" that appeared in pages 239-313 of the fourth volume, where the new generic nomen *Ichthyosaura* was proposed (p. 310), so this part, and the new nomen, must simply be credited to SONNINI & LATREILLE (1801*b*).

Another synonym of *Ichthyosaura* and *Mesotriton* overlooked by all authors until now is *Hemitriton* Dugès, 1852: 255. *ASW* states that the nucleospecies of this nomen has never been designated, but nevertheless places it in the synonymy of *Euproctus* Gene, 1839, which is both contradictory and twice erroneous. DUGÈS (1852) included six nominal species in his new genus *Hemitriton*: *Triton alpestris* Laurenti, 1768 from the Alps, *Hemitriton asper* Dugès, 1852 from the Pyrenees and five other nominal species from the latter mountains which he finally himself considered (DUGÈS, 1852: 267) as synonyms of the latter. By placing this nominal genus in the synonymy of *Euproctus*, *ASW* seems to imply that the genus was meant for the Pyrenean species, but then, if it was the case, the nomen should be placed in the synonymy of *Calotriton* Gray, 1858, not of *Euproctus*. But this is also wrong for ignoring a subsequent nucleospecies designation for this genus. Twenty years after the original description, FATIO (1872: 516) clearly designated *Triton alpestris* as the "type" of this taxon (which he treated as a subgenus of *Triton*) (**valid nucleospecies designation**), and expressed doubts (FATIO, 1872: 540) about the placement of the Pyrenean species in this genus. The nomen *Hemitriton* Dugès, 1852 is therefore a junior synonym of *Ichthyosaura* Sonnini & Latreille, 1801 (**new synonym**). It is preoccupied in zoology by *Hemitriton* Van der Hoeven, 1833: 305, a nomen that *ASW* qualifies as "*substitute name for* Hypochthon *Merrem*, Menobranchus *Harlan and* Siredon *Wagler*" and places in the synonymies of *Proteus* Laurenti, 1768, *Necturus* Rafinesque, 1819 and *Ambystoma* Tschudi, 1838. This is nomenclaturally impossible because, as stated above, a given nomen cannot be neonym for several distinct nomina and cannot appear in several synonymies. In fact, VAN DER HOEVEN (1833: 305) proposed his nomen *Hemitriton* for a *new genus* including three distinct subgenera, for which he used the nomina *Hypochthon* Merrem, 1820 (with two nominal species), *Menobranchus* Harlan, 1825 (with one nominal species) and *Siredon* Wagler, 1830 (with one nominal species). We hereby designate the nominal species *Proteus anguinus* Laurenti, 1768: 37 as nucleospecies of *Hemitriton* Van der Hoeven, 1833

(new nucleospecies designation), which will therefore now have to stand in the synonymy of *Proteus* Laurenti, 1768 as an objective synonym **(new synonym)**.

Genus **Lissotriton** Bell, 1839

Subgenus **Lissotriton** Bell, 1839

Nucleospecies. – *Salamandra punctata* Latreille, 1800, by subsequent designation of FITZINGER, 1843: 34.

Etymology. – From the Greek *lissos* ("smooth") and the generic nomen *Triton* Laurenti, 1768.

Grammatical gender. – Masculine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Lissotriton vulgaris* (Linnaeus, 1758) and excluding the species *Lissotriton boscai* (Lataste *in* BLANCHARD, 1879).

Diagnosis. – See table 2. See also table 1 for the diagnostic comparisons of the supraspecies *helveticus*, *italicus* and *vulgaris*, and table 4 for those of the six species of the latter supraspecies.

Idiognosis. – (1) TL 55-120 mm. (2) Habitus stout. Head elongated. (3) Ventral coloration variable, often with big black spots. Horizontal black line through eye usually present. (4) Sex dimorphism strong. Male usually much smaller than female, usually with crest on back. Female cloaca not conic. (5) Mostly terrestrial, breeding in lentic habitat. Whip and wave during nuptial dance of male, sometimes attenuated. (6) HAT. (7) Europe to Siberia.

Subgenus **Meinus** nov.

Nucleospecies. – *Pelonectes boscai* Lataste *in* BLANCHARD, 1879: 276, by present designation.

Etymology. – Unknown. Nomen borrowed from RAFINESQUE (1815: 78) who published it as a gymnonym. We have no clue on the meaning intended by its author for this nomen, except that it bears some resemblance to the Latin term *minus*, meaning "less".

Grammatical gender. – Masculine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Lissotriton boscai* (Lataste *in* BLANCHARD, 1879) and excluding the species *Lissotriton vulgaris* (Linnaeus, 1758).

Diagnosis. – See table 2.

Idiognosis. – (1) TL 70-100 mm. (2) Habitus stout. Head elongated. (3) Ventral coloration reddish-orange with black spots. Horizontal black line through eye absent. (4) Sex dimorphism strong. Male much smaller than female, without crest on the back. Female cloaca conic. (5) Very aquatic, in lentic habitat. No whip and wave during nuptial dance of male. (6) LAT. (7) Western Iberian Peninsula.

Comments. – The case of the gymnonym "*Meinus*" Rafinesque, 1815 was briefly presented above. This nomen has never been "validated" since its creation, and is still unpreoccupied in zoological nomenclature. As we need a nomen for the subgenus of *Lissotriton* including the species *Lissotriton boscai* (see above), and as this nomen has always been associated with the concept of *Triturus* in its wide traditional acception, we decided to "validate" it for this subgenus, rather than coining a brand new nomen. In order to link both nomina "*Meinus*" Rafinesque, 1815 and *Meinus* nov. by an objective synonymy, we also hereby designate *Pelonectes boscai* Lataste *in* BLANCHARD, 1879: 276 as the nucleospecies of "*Meinus*" Rafinesque, 1815 (**new nucleospecies designation**). This nomen will therefore now have to stand in the synonymy of *Meinus* nov. (**new synonym**).

Several erroneous facts have been repeatedly copied in the literature regarding the nucleospecies of this subgenus. *ASW* mentions a nominal genus "*Pelonectes* Lataste *in* Tourneville, 1879", with the nucleospecies "*Pelonectes boscai* Lataste *in* Tourneville, 1879". If this was correct, this nomen "*Pelonectes* Lataste *in* Tourneville, 1879" would be a senior synonym of *Meinus* nov., although invalid for being a junior homonym of *Pelonectes* Fitzinger, 1843 and *Pelonectes* Gistel, 1848.

MERTENS & WERMUTH (1960*b*: 25), THORN (1969: 248), FROST (1985: 614), MONTORI & HERRERO (2004: 233) and GARCÍA-PARÍS et al. (2004: 593) also recognized a nominal species "*Pelonectes boscai* Lataste *in* Tourneville, 1879", but this is erroneous, for two distinct reasons. First, if the original description was indeed that published by TOURNEVILLE (1879), the author of the nomen would be "Tourneville", or "Lataste & Tourneville", because this paper clearly states that, whereas the original diagnosis that it reproduces had been written by Lataste, the complete description was written by Tourneville, at the request of Lataste himself (TOURNEVILLE, 1879: 69). However, this point is largely irrelevant, because the original description of the taxon had appeared earlier (BLANCHARD, 1879), in a work mentioned by TOURNEVILLE (1879: 71, footnote). This description appeared in the report of a meeting of the Société Zoologique de France which makes it quite clear that both the new nomen and the Latin diagnosis of the new species were written, not by the secretary of the meeting, Raphael Blanchard, but by the author of the oral communication, Fernand Lataste. The latter alone is therefore the author of the new nomen *Pelonectes boscai*, according to Art. 50.2 of the *Code*.

A second mistake, present in *ASW*, in GORHAM (1974: 24) and in GARCIA-PARÍS et al. (2004: 593), is the recognition of a nominal genus "*Pelonectes* Lataste in Tourneville, 1879". There exists no such nominal taxon, not even as "*Pelonectes* Lataste in Blanchard, 1879". LATASTE (*in* BLANCHARD, 1879: 275) clearly stated that he was borrowing the nomen *Pelonectes* from FITZINGER (1843) as this nomen had "*remained without use*" ("*demeuré sans emploi*"). The nucleospecies of *Pelonectes* Fitzinger, 1843: 33 is *Molge platycephala* Gravenhorst, 1829 by original designation, so that this generic nomen nowadays applies to the genus *Euproctus* Gene, 1839 which does not include the nominal species *Pelonectes boscai*, but this does not mean that Lataste created a new generic nomen: the erroneous allocation of a species to a genus does not result in the creation of a new junior homonymous nominal genus having this species as nucleospecies, because otherwise there would be dozens of thousands of such junior homonymous generic nomina in zootaxonomy!

As a consequence of this analysis, the generic nomen *Meinus* nov. is the first one ever available for the genus including *Pelonectes boscai*.

Genus **Neurergus** Cope, 1862

Comments A subjective synonym of the nomen of this genus is *Rhithrotriton* Nesterov, 1916. The site *ASW* states wrongly that its nucleospecies was never designated In fact, this generic nomen was created for a taxon including two new nominal taxa: the species *Rhithrotriton derjugini* and the subspecies *Rhithrotriton derjugini microspilotus* The latter taxon being of rank subspecies, and a single species being included in the taxon, *Rhithrotriton derjugini* is the nucleospecies of this genus by original monophory (**valid nucleospecies designation**) (see above for a general explanation of this situation)

Subgenus **Musergus** nov.

Nucleospecies. *Molge strauchii* Steindachner, 1888: 32, by present designation.

Etymology. From the Turkish *Mus* (name of the city which is the onymotope of the nucleospecies) and the final part (5 last letters) of the generic nomen *Neurergus* Cope, 1862

Grammatical gender. Masculine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Neurergus strauchii* (Steindachner, 1888) and excluding the species *Neurergus crocatus* (Cope, 1862)

Diagnosis. - See table 2

Idiognosis. (1) TL up to 190 mm (2) Habitus stout Body flattened. (3) Ventral coloration mainly dark, with median longitudinal orange band. (4) Sex dimorphism moderate. Coloration of side of tail in breeding male silver-blue (5) Reproduction in lotic habitat (6) HAT (7) Northern eastern Turkey

Subgenus **Neurergus** Cope, 1862

Nucleospecies. *Neurergus crocatus* Cope, 1862 343, by original specific monophory.

Etymology From the Greek *neuron* ("sinew, tendon") and *ergon* ("work")

Grammatical gender. – Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Neurergus crocatus* (Cope, 1862) and excluding the species *Neurergus strauchii* (Steindachner, 1888)

Diagnosis. See table 2

Idiognosis (1) TL 140 180 mm (2) Habitus stout. Body flattened (3) Ventral coloration bright (4) Sex dimorphism moderate Coloration of side of tail in breeding not silver blue (5) Reproduction in lotic or lentic habitat (6) LAT or HAT (7) Southern eastern Turkey, western Iran and northern Irak

Genus **Triturus** Rafinesque, 1815
Subgenus **Pyronicia** Gray, 1858

Nucleospecies. – *Salamandra marmorata* Latreille, 1800: 29, by present designation.

Etymology. – Probably from the Greek *pur* ("fire") and *nikao* ("I prevail, I am victorious"), possibly meaning that in Europe salamanders have long been believed to cross fire and survive.

Grammatical gender. – Feminine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Triturus marmoratus* (Latreille, 1800) and excluding the species *Triturus cristatus* (Laurenti, 1768).

Diagnosis. – See table 2.

Idiognosis. – (1) TL 100-180 mm. (2) Habitus stout. Head wide. Skin very granular. (3) Dorsal coloration green. Ventral coloration black and white. (4) Sex dimorphism strong. Dorsal crest of breeding male undulating. (5) Highly terrestrial. (6) LAT. (7) Western Europe.

Comments. – Until this work, no nomen was clearly available for this subgenus, but three genus-series nomina that can apply to this group were still awaiting a designation of nucleospecies, so that one of them can be resurrected for this purpose: *Hemisalamandra* Dugès, 1852, *Pyronicia* Gray, 1858, and *Neotriton* Bolkay, 1927. We chose the second of these three nomina because it is one of the shortest two (9 letters vs. respectively 14 and 9) and it sounds to us by far the most euphonious of the three. Besides, at least to a French reader, the nomen *Pyronicia* carries a message of beauty and "nobleness" that fully applies, in our opinion, to the majestic species *Triturus marmoratus* and its allies. Let us consider these three nomina successively.

The generic nomen *Hemisalamandra* Duges, 1852: 254, 256 appears in *ASW* in the synonymies of both *Lissotriton* and *Triturus*. This nomen was created by DUGES (1852) with eleven originally included nominal species, two considered valid (*Salamandra marmorata* Latreille, 1800 and *Triton cristatus* Laurenti, 1768), and nine considered their synonyms (one of the former, eight of the latter), some of which are indeed now referred to the genus *Lissotriton*. Designating *Salamandra marmorata* as the nucleospecies of this genus would validate a nomen which is not only 14 letters long, but also misleading in suggesting that this genus belongs in the "true salamanders" rather than in the "newts". We therefore designate hereby *Triton cristatus* Laurenti, 1768: 39 as the nucleospecies of *Hemisalamandra* Duges, 1852 (**new nucleospecies designation**). This nomen will therefore permanently stand in the synonymy of *Triturus* Rafinesque, 1815 as an objective synonym (**new synonym**).

The generic nomen *Pyronicia* Gray, 1858: 140 also appears in *ASW* in the synonymies of both *Lissotriton* and *Triturus*. It was created with four originally included nominal species, two considered valid (*Salamandra marmorata* Latreille, 1800 and *Salamandra punctata* Latreille, 1800), and two considered synonyms of the latter (the last three being now members of the hyponymous subgenus *Lissotriton*). We hereby designate *Salamandra marmorata* Latreille, 1800: 29 as the nucleospecies of *Pyronicia* Duges, 1858 (**new nucleospecies designation**), which consequently becomes the valid nomen for the subgenus including it and its close allies.

The nomen *Neotriton* Bolkay, 1927: 65 was created at subgeneric rank within *Triton* Laurenti, 1768, without nucleospecies designation, but with mention of at least four included taxa among at least six, as two of these taxa were given the rank subspecies and no other subspecies of the same species was cited. The four nominal species cited are *Triton blasii* De l'Isle du Dreneuf, 1862, *Triton cristatus* Laurenti, 1768, *Triton karelinii* Strauch, 1870 and *Salamandra marmorata* Latreille, 1800. We hereby designate *Triton karelinii* Strauch, 1870: 42 as nucleospecies of this nominal genus (**new nucleospecies designation**). This nomen will therefore now have to stand in the synonymy of the hyponymous subgenus *Triturus* Rafinesque, 1815 as a subjective synonym (**new synonym**).

Subgenus **Triturus** Rafinesque, 1815

Nucleospecies. – *Triton cristatus* Laurenti, 1768: 39, by subsequent designation of Fitzinger (1843: 34) under *Triton* Laurenti, 1768: 37.

Etymology. – Apparently directly derived from the generic nomen *Triton* Laurenti, 1768: 37. The ending *-urus* reminds the Greek root *oura* ("tail") but is unkilely to be part of the etymology of *Triturus*, as the latter term would then mean "having a tail of *Triton*", i.e., having its own tail!

Grammatical gender. – Masculine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Triturus marmoratus* (Latreille, 1800).

Diagnosis. – See table 2.

Idiognosis. – (1) TL 160-180 mm. (2) Habitus slender. Head narrow. Skin granular. (3) Dorsal coloration black. Ventral coloration yellow or orange with black spots. (4) Sex dimorphism strong. Dorsal crest of breeding male denticulated. (5) Rather aquatic. (6) HAT. (7) Europe to Caucasus and Iran.

Comments. – As discussed above, the nomen *Triturus* Rafinesque, 1815 is a neonym for *Triton* Laurenti, 1768. The latter being preoccupied, *Triturus* is the valid nomen for the genus, having priority over the other three neonyms subsequently published for *Triton* Laurenti, 1768 (*Molge* Merrem, 1820, *Oiacurus* Leuckart, 1821, *Tritonella* Swainson, 1839). Its nucleospecies is *Triton cristatus* Laurenti, 1768 by subsequent designation, under *Triton*, of Fitzinger (1843: 34). This nomen has several other synonyms. *Petraponia* Massalongo, 1853: 14 (nucleospecies, *Petraponia nigra* Massalongo, 1853: 15, by original specific monophory), *Turanomolge* Nikosky, 1918: 182 (nucleospecies, by original specific monophory, *Turanomolge mensbieri* Nikolsky, 1918: 182), *Alethotriton* Fatio, 1872: 517, and *Neotriton* Bolkay, 1927: 65. The nucleospecies of the latter two have not been properly identified so far, thus requiring a brief discussion.

Concerning the subgeneric nomen *Alethotriton* Fatio, 1872, *ASW* writes: "*Type species*: Triton cristatus *Laurenti, 1768, by implication*". As reminded above, the *Code* does not recognize nucleospecies designations "*by implication*", so this information is incorrect. In fact, Fatio (1872: 516, 518) had twice expressly written that the nominal species

Triton cristatus Laurenti, 1768 was the "type" of this subgenus, thus making an original nucleospecies designation (**valid nucleospecies designation**). This nomen is therefore an invalid junior objective synonym of *Triturus* Rafinesque, 1815 (**new synonym**)

As for the nomen *Neotriton* Bolkay, 1927, it was discussed above under *Pyronicia*.

Subtribus *TARICHINA* nov

Nucleogenus. *Taricha* Gray, 1850: 5, 15, by present designation.

Entexognosis The most inclusive holophyletic taxon including the species *Taricha torosa* (Rathke, 1833) and excluding the species *Triturus cristatus* (Laurenti, 1768).

Diagnosis. See table 2.

Idiognosis. – (1) TL 100-220 mm (2) Habitus stout. (3) Dorsal and ventral colorations very contrasted. (4) Sex dimorphism strong. Dorsal crest absent. (5) Breeding habitat lentic or lotic. Type III amplexus. (6) HAT. (7) Nearctic.

Genus **Notophthalmus** Rafinesque, 1820

Subgenus **Notophthalmus** Rafinesque, 1820

Nucleospecies. – *Triturus miniatus* Rafinesque, 1820: 5, by original specific monophory.

Etymology From the Greek *notos* ("the back") and *ophthalmos* ("eye").

Grammatical gender. – Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Notophthalmus miniatus* Rafinesque, 1820 and excluding the species *Notophthalmus meridionalis* (Cope, 1880).

Diagnosis. See table 2.

Idiognosis (1) TL 90-140 mm (2) Habitus stout (3) Dorsal coloration light-olive green, sometimes with red spots or lines, ventral coloration orange to yellow, both with small black spots. (4) Sex dimorphism strong Black horny ridges present on thighs of male. (5) Very aquatic, breeding in cold water (6) HAT (7) Eastern North America (8) Eft stage and neoteny present.

Subgenus **Rafinus** nov.

Nucleospecies *Diemictylus miniatus meridionalis* Cope, 1880: 30, by present designation

Etymology From the patronym of the naturalist Constantin Samuel Rafinesque-Schmaltz, who was born in Constantinople (now Istanbul) in 1783 and died in 1840 in Philadelphia after an extraordinary life which would be worth several novels and movies (RAFINESQUE, 1836, WARREN 2004), and who contributed to the discovery and naming of many species of amphibians, in particular urodelans, in Europe and North America.

Grammatical gender. Masculine.

Entexognosis. The most inclusive holophyletic taxon including the species *Notophthalmus meridionalis* (Cope, 1880) and excluding the species *Notophthalmus miniatus* Rafinesque, 1820.

Diagnosis. – See table 2.

Idiognosis. (1) TL 100-110 mm. (2) Habitus stout. (3) Dorsal coloration olive green, without red coloration; ventral coloration orange to yellow, both with large black spots. (4) Sex dimorphism moderate. No transverse black horny ridges on thighs of male. (5) Aquatic only during breeding period, in warm water. (6) HAT. (7) Texas and north-eastern Mexico. (8) No eft stage, no neoteny.

Genus **Taricha** Gray, 1850

Subgenus **Taricha** Gray, 1850

Nucleospecies. *Triton torosa* Rathke, 1833: 12, by original specific monophory.

Etymology. From the Greek *tarikhos*, "mummy", probably because of the rough skin of these animals.

Grammatical gender. – Feminine.

Entexognosis. The most inclusive holophyletic taxon including the species *Taricha torosa* (Rathke, 1833) and excluding the species *Taricha rivularis* (Twitty, 1935).

Diagnosis. – See table 2.

Idiognosis. (1) TL up to 220 mm. (2) Habitus stout. (3) Dorsal coloration brown, ventral coloration yellow-orange. Iris yellow. (4) Sex dimorphism strong. (5) Many eggs deposited in lentic habitat or few eggs deposited in lotic or lentic habitat. (6) HAT. (7) Western United States of America and western Canada.

Subgenus **Twittya** nov.

Nucleospecies. *Triturus rivularis* Twitty, 1935: 73, by present designation.

Etymology. From the patronym of Victor Chandler Twitty (1901-1967), who contributed to the knowledge of North American urodelans, in particular of the genus *Taricha*, and wrote the nice little book *Of scientists and salamanders* (TWITTY, 1966).

Grammatical gender. – Feminine.

Entexognosis. The most inclusive holophyletic taxon including the species *Taricha rivularis* (Twitty, 1935) and excluding the species *Taricha torosa* (Rathke, 1833).

Diagnosis. – See table 2.

Idiognosis. (1) TL up to 190 mm. (2) Habitus stout. (3) Dorsal coloration black, ventral coloration tomato red. Iris black. (4) Sex dimorphism rather weak. (5) Few eggs deposited in lotic habitat. (6) HAT. (7) Western United States of America.

Tribus *PLEURODELINI* Tschudi, 1838

Nucleogenus. *Pleurodeles* Michahelles, 1830: 195, by implicit etymological designation

Entexognosis The most inclusive holophyletic taxon including the species *Triturus cristatus* (Laurenti, 1768) and excluding the species *Pleurodeles waltl* (Michahelles, 1830).

Diagnosis. – See table 2.

Genus **Tylototriton** Anderson, 1871

Subgenus **Tylototriton** Anderson, 1871

Nucleospecies *Tylototriton verrucosus* Anderson, 1871: 423, by original specific monophory.

Etymology. – From the Greek *tulos* ("swelling") and the generic nomen *Triton* Laurenti, 1768

Grammatical gender. – Masculine.

Entexognosis. The most inclusive holophyletic taxon including the species *Tylototriton verrucosus* Anderson, 1871 and excluding the species *Tylototriton asperrimus* (Unterstein, 1830)

Diagnosis See table 2

Idiognosis (1) TL 160-230 mm (2) Habitus stout Cephalic ridges very developed. Vertebral ridge sharp. (3) Dorsal coloration usually rather bright, ventral coloration black to light (4) Sex dimorphism strong (5) Aquatic during breeding period Eggs rather small, deposited in water (6) HAT (7) Bhutan, China, India, Laos, Myanmar, Nepal, Thailand

Subgenus **Yaotriton** nov

Nucleospecies *Tylototriton asperrimus* Unterstein, 1830: 314, by present designation

Etymology From the Chinese *Yao* (name of the mountain, the Yao Shan, which is the onymotope of the nucleospecies) and the generic nomen *Triton* Laurenti, 1768

Grammatical gender. – Masculine.

Entexognosis The most inclusive holophyletic taxon including the species *Tylototriton asperrimus* (Unterstein, 1830) and excluding the species *Tylototriton verrucosus* Anderson, 1871

Diagnosis See table 2

Idiognosis (1) TL 120-160 mm (2) Habitus stout Cephalic ridges very developed Vertebral ridge very sharp. (3) Dorsal coloration black, ventral coloration black (4) Sex dimorphism weak (5) Terrestrial Eggs large, deposited on land or in contact with water (6) LAT (7) Central and southern China, Vietnam.

Subfamilia *SALAMANDRINAE* Goldfuss, 1820

Nucleogenus. *Salamandra* Laurenti, 1768: 41, by implicit etymological designation.

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra salamandra* (Linnaeus, 1758) and excluding the species *Pleurodeles waltl* (Michahelles, 1830) and *Salamandrina perspicillata* (Savi, 1821)

Diagnosis. – See table 1.

Tribus *CHIOGLOSSINI* nov.

Nucleogenus – *Chioglossa* Bocage, 1864: 264, by present designation

Entexognosis The most inclusive holophyletic taxon including the species *Chioglossa lusitanica* Bocage, 1864 and excluding the species *Salamandra salamandra* (Linnaeus, 1758).

Diagnosis. See table 2

Idiognosis. – (1) TL 150-200 mm. (2) Habitus slender. Tail very long. (3) Dorsal coloration dull with bright stripe or spots, ventral coloration dull (4) Sex dimorphism strong, much longer tail in male. Forearm of breeding male enlarged (5) Aquatic during breeding period. Eggs deposited in water (6) LAT (7) Western Iberian Peninsula, western Caucasus and north-eastern Turkey.

Tribus *SALAMANDRINI* Goldfuss, 1820

Nucleogenus. *Salamandra* Laurenti, 1768: 41, by implicit etymological designation

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra salamandra* (Linnaeus, 1758) and excluding the species *Chioglossa lusitanica* Bocage, 1864.

Diagnosis See table 2

Idiognosis. (1) TL 110-320 mm (2) Habitus stout Tail short. (3) Dorsal coloration usually bright with spots or bands, ventral coloration dull (4) Sex dimorphism moderate Forearm of breeding male not enlarged (5) Terrestrial, even during breeding period. Eggs deposited in water or retained in female (ovoviviparity or viviparity). (6) Usually HAT. (7) Western Palaearctic.

Genus **Salamandra** Laurenti, 1768

Subgenus **Algiandra** nov.

Nucleospecies *Salamandra maculosa* var. *algira* Bedriaga, 1883: 252, by present designation.

Etymology. – From the first four letters of the old German *Algierien* ("Algeria", name of the country including the onymotope of the nucleospecies) and the last five letters of the generic nomen *Salamandra* Laurenti, 1768

Table 4 Diagnostic comparisons among two groups composed of six parordinate taxa as recognized here

Superordinate taxon	**Supraspecies *Lissotriton (Lissotriton) vulgaris* (Linnaeus, 1758)**					
Parordinate taxa	**Species *Lissotriton graecus* (Wolterstorff, 1905)**	**Species *Lissotriton kosswigi* (Freytag, 1955)**	**Species *Lissotriton lantzi* (Wolterstorff, 1914)**	**Species *Lissotriton meridionalis* (Boulenger, 1882)**	**Species *Lissotriton montandoni* (Boulenger, 1880)**	**Species *Lissotriton vulgaris* (Linnaeus, 1758)**
Size of male	Small to large TL 75-100 mm)	Small (TL 70-80 mm)	Large (TL 75-110 mm)	Small (TL 60-80 mm)	Large (TL 70-100 mm)	Large (TL 100-110 mm
Habitus	Stout	Rather stout	Stout	Slender	Stout	Stout
Development of dorsal crest in breeding male	Low	Medium	High	Low	Low	High
Beginning of dorsal crest in breeding male	Back of head	Level of forelimbs	Back of head	Back of head	Back of head	Back of head
Shape of dorsal crest in breeding male	Straight	Straight	Undulating	Straight	Straight	Undulating
Dorsolateral ridge in breeding male	Present	Very sharp	Weak	Present	Very sharp	Absent
Palm or fringe on toes in breeding male	Moderate	Large	Large	Small	Absent	Very small
Tail fin in breeding male	Present (to 7 mm)	Present (to 9 mm)	Present (to 7 mm)	Present (to 8 mm)	Present (to 4 mm)	Absent
Size of rounded spots on male dorsum	Large	Large	Large	Small	Absent	Large or small
Colour of rounded spots on male venter	Blue-black	Blue-black	Black	Black	Absent	Black
Habitat	Mostly aquatic	Mostly aquatic	Mostly aquatic	Mostly aquatic	Mostly terrestrial	Mostly terrestrial
Adaptability in terrarium	HAT	LAT	HAT	LAT	LAT	HAT
Superordinate taxon	**Genus *Salamandra* Laurenti, 1768**					
Parordinate taxa	**Subgenus *Algiandra* nov**	**Subgenus *Alpandra* nov.**	**Subgenus *Corsandra* nov.**	**Subgenus *Mimandra* nov.**	**Subgenus *Oriandra* nov.**	**Subgenus *Salamandra* Laurenti, 1768**
Size	Medium to large	Small	Large	Medium	Large	Small to large
Dorsolateral or lateral glands	Dorsolateral	Dorsolateral	Dorsolateral	Lateral	Dorsolateral	Dorsolateral
Head	Narrow, small	Narrow, medium	Wide, large	Wide, medium	Wide, medium to large	Narrow to wide small to medium
Snout	Pointed	Rounded	Rounded	Pointed	Rounded to moderately pointed	Pointed to rounded
Dorsal coloration	With yellow or red colour	Black or yellowish	With yellow colour	Black	With yellow colour	With yellow, orange or red colour
Reproduction mode	Ovoviviparity lecithotroph or viviparity adelphotroph	Viviparity matrotroph	Ovoviviparity lecithotroph	Viviparity matrotroph	Ovoviviparity lecithotroph	Ovoviviparity lecithotroph or viviparity adelphotroph
Adaptability in terrarium	LAT or HAT	LAT or HAT	HAT	LAT	Unknown	LAT or HAT

Grammatical gender - Feminine.

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra algira* (Bedriaga, 1883) and excluding the species *Salamandra atra* Laurenti, 1768, *Salamandra corsica* Savi, 1838, *Salamandra infraimmaculata* Martens, 1885, *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and *Salamandra salamandra* (Linnaeus, 1758).

Diagnosis. See table 4. See also table 2 for the diagnostic comparisons of the species *Salamandra algira* and *Salamandra tingitana*

Idiognosis (1) TL up to 230 mm (2) Head narrow and small, snout pointed Dorsolateral glands. (3) Yellow spots, mainly regular, sometimes attenuated, sometimes red coloration on dorsal surfaces. (4) Sex dimorphism moderate (5) Ovoviviparous lecithotroph or viviparous adelphotroph (6) Usually LAT, HAT in *Salamandra tingitana* (7) Northern Africa.

Subgenus **Alpandra** nov

Nucleospecies *Salamandra atra* Laurenti, 1768 42, by present designation.

Etymology. From the Latin *Alpes* (name of the mountains including the onymotope of the nucleospecies) and the last five letters of the generic nomen *Salamandra* Laurenti, 1768

Grammatical gender. – Feminine

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra atra* Laurenti, 1768 and excluding the species *Salamandra algira* (Bedriaga, 1883), *Salamandra corsica* Savi, 1838, *Salamandra infraimmaculata* Martens, 1885, *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and *Salamandra salamandra* (Linnaeus, 1758).

Diagnosis. See table 4 See also table 2 for the diagnostic comparisons of the species *Salamandra atra* and *Salamandra aurorae*.

Idiognosis (1) TL 130 mm (2) Head narrow and medium, snout rounded. Dorsolateral glands. (3) Black or yellow bands. (4) Sex dimorphism moderate (5) Viviparous matrotroph (6) Usually LAT, HAT in *Salamandra aurorae*. (7) Alps.

Subgenus **Corsandra** nov.

Nucleospecies *Salamandra corsica* Savi, 1838 208, by present designation

Etymology From the Latin *Corsica* (name of the island including the onymotope of the nucleospecies) and the last five letters of the generic nomen *Salamandra* Laurenti, 1768

Grammatical gender. Feminine

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra corsica* Savi, 1838 and excluding the species *Salamandra algira* (Bedriaga, 1883), *Salamandra atra* Laurenti, 1768, *Salamandra infraimmaculata* Martens, 1885, *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and *Salamandra salamandra* (Linnaeus, 1758).

Diagnosis. – See table 4

Idiognosis. (1) TL up to 250 mm (2) Head wide and large, snout rounded. Dorsolateral glands. (3) Many yellow spots, irregular (4) Sex dimorphism moderate (5) Ovoviviparous lecithotroph. (6) HAT. (7) Corsica

Subgenus **Mimandra** nov

Nucleospecies *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988: 619, by present designation

Etymology From the Latin *mima* ("actress, female mime") and the last five letters of the generic nomen *Salamandra* Laurenti, 1768 This nomen points to the fact that the nucleospecies of this subgenus was long confounded with the species *Salamandra atra* Laurenti, 1768, which is similar to it by its coloration, its reproductive mode (viviparity) and its Alpine distribution, before being discovered to resemble it by convergence.

Grammatical gender – Feminine.

Entexognosis. – The most inclusive holophyletic taxon including the species *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and excluding the species *Salamandra algira* (Bedriaga, 1883), *Salamandra atra* Laurenti, 1768, *Salamandra infraimmaculata* Martens, 1885, *Salamandra corsica* Savi, 1838 and *Salamandra salamandra* (Linnaeus, 1758)

Diagnosis. – See table 4.

Idiognosis (1) TL 160 mm (2) Head wide and medium, snout pointed. Lateral glands. (3) Black. (4) Sex dimorphism moderate. (5) Viviparous matrotroph (6) LAT. (7) South-western Alps.

Subgenus **Oriandra** nov.

Nucleospecies. *Salamandra maculosa* var. *infraimmaculata* Martens, 1885, 195, by present designation.

Etymology. From the first three letters of Latin *oriens* ("the East") and the last five letters of the generic nomen *Salamandra* Laurenti, 1768.

Grammatical gender. – Feminine.

Entexognosis The most inclusive holophyletic taxon including the species *Salamandra infraimmaculata* Martens, 1885 and excluding the species *Salamandra algira* (Bedriaga, 1883), *Salamandra atra* Laurenti, 1768, *Salamandra corsica* Savi, 1838, *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988 and *Salamandra salamandra* (Linnaeus, 1758)

Diagnosis See table 4

Idiognosis (1) TL up to 324 mm (2) Head wide, medium to large, snout rounded to moderately pointed Dorsolateral glands. (3) Many yellow spots, regular or irregular, very large or very small. (4) Sex dimorphism moderate (5) Ovoviviparous lecithotroph (6) Adaptability in captivity unknown. (7) From Israel to western Iran.

Subgenus **Salamandra** Laurenti, 1768

Nucleospecies *Salamandra maculosa* Laurenti, 1768 42, by subsequent designation of FITZINGER, 1843, 33

Etymology – From the Latin *salamandra* ("salamander")

Grammatical gender. – Feminine.

Entexognosis. The most inclusive holophyletic taxon including the species *Salamandra salamandra* (Linnaeus, 1758) and excluding the species *Salamandra algira* (Bedriaga, 1883), *Salamandra atra* Laurenti, 1768, *Salamandra corsica* Savi, 1838, *Salamandra infraimmaculata* Martens, 1885 and *Salamandra lanzai* Nascetti, Andreone, Capula & Bullini, 1988.

Diagnosis See table 4. See also table 1 for the diagnostic comparisons of the species *Salamandra almanzoris*, *Salamandra longirostris* and *Salamandra salamandra* and of the exerges *crespoi*, *fastuosa* and *salamandra* of the latter species.

Idiognosis. – (1) TL 111-280 mm. (2) Head narrow to wide, small to medium, snout pointed to rounded. Dorsolateral glands. (3) Spots or bands, yellow or sometimes orange. (4) Sex dimorphism moderate. (5) Ovoviviparous lecithotroph or viviparous adelphotroph. (6) LAT or HAT. (7) Southern and central Europe.

Comments. – Following STEJNEGER (1936: 135), FROST (1985: 613) stated erroneously that the nucleospecies of this nominal genus was "*Salamandra maculosa* Laurenti, 1768 (= *Lacerta salamandra* Linnaeus, 1758) by tautonymy". MONTORI & HERRERO (2004: 55) also considered *Lacerta salamandra* Linnaeus, 1758 as the nucleospecies of this genus. However, as pointed out by DUBOIS (1987*c*: 136-137), this is impossible, as the nominal species *Lacerta salamandra* Linnaeus, 1758 was not part of the nominal species originally included in the genus. Nucleospecies of nominal genera are nominal species, not taxonomic species, and the synonymy between both nomina *Salamandra maculosa* Laurenti, 1768 and *Lacerta salamandra* Linnaeus, 1758 is subjective, even if widely accepted for two centuries, therefore liable to change. The valid designation of *Salamandra maculosa* Laurenti, 1768 as nucleospecies of this genus was made by FITZINGER (1843: 33) (**valid nucleospecies designation**).

A nomen which should stand in the synonymy of this genus is "*Salamandra*" Gronovius, 1763: 12 (**new synonym**). This is an anoplonym, as having been published in a work not using a binominal nomenclature for species (ANONYMOUS, 1925). In order to stabilize the place of this nomen in synonymies, we hereby designate *Salamandra maculosa* Laurenti, 1768 as its nucleospecies (**new nucleospecies designation**).

Subfamilia *SALAMANDRININAE* Fitzinger, 1843

Nucleogenus. - *Salamandrina* Fitzinger, 1826: 41, by implicit etymological designation.

Entexognosis. – The most inclusive holophyletic taxon including the species *Salamandrina perspicillata* (Savi, 1821) and excluding the species *Pleurodeles waltl* (Michahelles, 1830) and *Salamandra salamandra* (Linnaeus, 1758).

Diagnosis. – See table 1.

CONCLUSION

The ergotaxonomy of the family *SALAMANDRIDAE* here proposed (table 5) recognizes 253 taxa at 11 different ranks, including 118 species and 60 subspecies, grouped in 31 genera and 23 subgenera. From family to subspecies, the increase in the number of taxa at the four major ranks (family, genus, species and subspecies) is regular, as shown in fig. 2. This suggests that this ergotaxonomy is rather well balanced, at least as measured by the quantitative "metataxonomic criterion" described by VAN VALEN (1973) and DUBOIS (1988*a-b*), but of course by itself this information does not mean that this taxonomy is "valid" by any other criterion.

Table 5. A complete ergotaxonomy of the family *SALAMANDRIDAE* Goldfuss, 1820. Nomina of the family-series are printed in *CAPITAL ITALICS* and those of the genus- and species-series in *italics*. Abbreviations for ranks: sF, subfamilia, T, tribus; sT, subtribus, iT, infratribus; G, genus, sG, subgenus, SS, supraspecies; S, species; E, exerge; sS, subspecies.

sF	**T**	**sT**	**iT**	**G**	**sG**	**SS**	**S**	**E**	**sS**
PLEURODELINAE Tschudi, 1838									
	MOLGINI Gray, 1850								
		MOLGINA Gray, 1850							
			CYNOPITA nov.						
				† *Carpathotriton* Venczel, 2008					
							† *Carpathotriton matraensis* Venczel, 2008		
				Cynops Tschudi, 1838					
							Cynops ensicauda (Hallowell, 1860)		
									Cynops ensicauda ensicauda (Hallowell, 1860)
									Cynops ensicauda popei (Inger, 1947)
							Cynops pyrrhogaster (Boie, 1826)		
				Hypselotriton Wolterstorff, 1934					
					Hypselotriton Wolterstorff, 1934				
							Hypselotriton (Hypselotriton) chenggongensis (Kou & Xing, 1983)		
							Hypselotriton (Hypselotriton) cyanurus (Liu, Hu & Yang, 1962)		
									Hypselotriton (Hypselotriton) cyanurus cyanurus (Liu, Hu & Yang, 1962)
									Hypselotriton (Hypselotriton) cyanurus yunnanensis (Yang, 1983)
							Hypselotriton (Hypselotriton) wolterstorffi (Boulenger, 1905)		
					Pingia Chang, 1935				
							Hypselotriton (Pingia) granulosus (Chang, 1933)		
							Hypselotriton (Pingia) orientalis (David, 1875)		
							Hypselotriton (Pingia) orphicus (Risch, 1983)		
				Laotriton nov.					
							Laotriton laoensis (Stuart & Papenfuss, 2002)		
				Pachytriton Boulenger, 1878					
							Pachytriton archospotus Shen, Shen & Mo, 2008		
							Pachytriton brevipes (Sauvage, 1876)		
							Pachytriton labiatus (Unterstein, 1930)		
				Paramesotriton Chang, 1935					
					Allomesotriton Freytag, 1983				
							Paramesotriton (Allomesotriton) caudopunctatus (Liu & Hu *in* HU, DJAO & LIU, 1973)		
					Paramesotriton Chang, 1935				
							Paramesotriton (Paramesotriton) chinensis (Gray, 1859)		
							Paramesotriton (Paramesotriton) deloustali (Bourret, 1934)		
							Paramesotriton (Paramesotriton) fuzhongensis Wen, 1989		
							Paramesotriton (Paramesotriton) guangxiensis (Huang, Tang & Tang, 1983)		
							Paramesotriton (Paramesotriton) hongkongensis (Myers & Leviton, 1962)		
							Paramesotriton (Paramesotriton) longliensis Li, Tian, Gu & Xiong, 2008		
							Paramesotriton (Paramesotriton) zhijinensis Li, Tian & Gu, 2008		
				† *Procynops* Young, 1965					
							† *Procynops miocenicus* Young, 1965		
			EUPROCTITA nov.						
				Euproctus Gené, 1838					
							Euproctus montanus (Savi, 1838)		
							Euproctus platycephalus (Gravenhorst, 1829)		
			MOLGITA Gray, 1850						
				Incertae sedis					
							† *Triturus lacasianus* Lartet, 1851		
							† *Triturus minimus* Giebel, 1847		
							† *Triturus sansaniensis* Lartet, 1851		
							† *Triturus wintershofi* Lunau, 1950		

Table 5. – (continued 1).

sF	T	sT	iT	G	sG	SS	S	E	sS
				Calotriton Gray, 1858					
							Calotriton arnoldi Carranza & Amat, 2005		
							Calotriton asper (Duges, 1852)		
				Ichthyosaura Sonnini & Latreille, 1801					
							Ichthyosaura alpestris (Laurenti, 1768)		
								alpestris (Laurenti, 1768)	
									Ichthyosaura alpestris (alpestris) alpestris (Laurenti, 1768)
									Ichthyosaura alpestris (alpestris) apuana (Bonaparte, 1839)
									Ichthyosaura alpestris (alpestris) cyreni (Wolterstorff, 1932)
									Ichthyosaura alpestris (alpestris) inexpectata (Dubois & Breuil, 1983)
								reiseri (Werner, 1902)	
									Ichthyosaura alpestris (reiseri) carpathica (Dely, 1959)
									Ichthyosaura alpestris (reiseri) montenegrina (Radovanovic, 1951)
									Ichthyosaura alpestris (reiseri) reiseri (Werner, 1902)
									Ichthyosaura alpestris (reiseri) veluchiensis (Wolterstorff, 1935)
				† *Koalliella* Herre, 1950					
							† *Koalliella genzeli* Herre, 1950		
				Lissotriton Bell, 1839					
					Incertae sedis				
							† *Lissotriton opalinus* (Meyer, 1851)		
							† *Lissotriton rohrsi* (Herre, 1955)		
					Lissotriton Bell, 1839				
						helveticus (Razoumowsky, 1789)			
							Lissotriton (Lissotriton) (helveticus) helveticus (Razoumowsky, 1789)		
									Lissotriton (Lissotriton) (helveticus) helveticus alonsoi (Seoane, 1884)
									Lissotriton (Lissotriton) (helveticus) helveticus helveticus (Razoumowsky, 1789)
									Lissotriton (Lissotriton) (helveticus) helveticus punctillatus (Schmidtler, 1970)
						italicus (Peracca, 1898)			
							Lissotriton (Lissotriton) (italicus) italicus (Peracca, 1898)		
									Lissotriton (Lissotriton) (italicus) italicus italicus (Peracca, 1898)
									Lissotriton (Lissotriton) (italicus) italicus molisanus (Altobello, 1926)
						vulgaris (Linnaeus, 1758)			
							Lissotriton (Lissotriton) (vulgaris) graecus (Wolterstorff, 1905)		
							Lissotriton (Lissotriton) (vulgaris) kosswigi (Freytag, 1955)		
							Lissotriton (Lissotriton) (vulgaris) lantzi (Wolterstorff, 1914)		
							Lissotriton (Lissotriton) (vulgaris) meridionalis (Boulenger, 1882)		
							Lissotriton (Lissotriton) (vulgaris) montandoni (Boulenger, 1880)		
							Lissotriton (Lissotriton) (vulgaris) vulgaris (Linnaeus, 1758)		
									Lissotriton (Lissotriton) (vulgaris) vulgaris ampelensis (Fuhn, 1951)
									Lissotriton (Lissotriton) (vulgaris) vulgaris vulgaris (Linnaeus, 1758)
					Meinus nov.				
							Lissotriton (Meinus) boscai (Lataste in BLANCHARD, 1879)		
							Lissotriton (Meinus) maltzani (Boettger, 1879)		
				Neurergus Cope, 1862					
					Musergus nov				
							Neurergus (Musergus) strauchii (Steindachner, 1888)		
									Neurergus (Musergus) strauchii barani Oz, 1994
									Neurergus (Musergus) strauchii strauchii (Steindachner, 1888)
					Neurergus Cope, 1862				
							Neurergus (Neurergus) crocatus Cope, 1862		
							Neurergus (Neurergus) kaiseri Schmidt, 1952		
							Neurergus (Neurergus) microspilotus (Nesterov, 1916)		
				† *Oligosemia* Navas, 1922					
							† *Oligosemia spinosa* Navas, 1922		

Table 5. – (continued 2)

sF T sT iT G sG SS S E sS

    - *Ommatotriton* **Gray**, 1850
        - *Ommatotriton ophryticus* (Berthold, 1846)
            - *Ommatotriton ophryticus nesterovi* Litvinchuk, Zuiderwijk, Borkin & Rosanov, 2005
            - *Ommatotriton ophryticus ophryticus* (Berthold, 1846)
        - *Ommatotriton vittatus* (Gray, 1835)
            - *Ommatotriton vittatus cilicensis* (Wolterstorff 1906)
            - *Ommatotriton vittatus vittatus* (Gray, 1835)
    - ***Triturus*** **Rafinesque**, 1815
      - *Pyronicia* **Gray**, 1858
        - ***Triturus*** *(Pyronicia) marmoratus* (Latreille, 1800)
        - ***Triturus*** *(Pyronicia) pygmaeus* (Wolterstorff, 1905)
      - ***Triturus*** **Rafinesque**, 1815
        - ***Triturus*** *(Triturus) carnifex* (Laurenti, 1768)
        - ***Triturus*** *(Triturus) cristatus* (Laurenti, 1768)
        - ***Triturus*** *(Triturus) dobrogicus* (Kiritzescu, 1903)
            - *Triturus (Triturus) dobrogicus dobrogicus* (Kiritzescu, 1903)
            - *Triturus (Triturus) dobrogicus macrosoma* (Boulenger, 1908)
        - ***Triturus*** *(Triturus) karelinii* (Strauch, 1870)
            - *Triturus (Triturus) karelinii arntzeni* Litvinchuk, Borkin, Dzukić & Kalezic 1999
            - *Triturus (Triturus) karelinii karelinii* (Strauch, 1870)
        - ***Triturus*** *(Triturus) macedonicus* (Karaman, 1922)
  - ***TARICHINA*** **nov.**
    - ***Notophthalmus*** **Rafinesque**, 1820
      - **Incertae sedis**
        - † ***Notophthalmus*** *crassus* Tihen, 1974
        - † ***Notophthalmus*** *robustus* Estes, 1963
      - ***Notophthalmus*** Rafinesque 1820
        - ***Notophthalmus*** *(Notophthalmus) perstriatus* (Bishop, 1941)
        - ***Notophthalmus*** *(Notophthalmus) viridescens* (Rafinesque 1820)
            - *Notophthalmus (Notophthalmus) viridescens dorsalis* (Harlan, 1828)
            - *Notophthalmus (Notophthalmus) viridescens louisianensis* Wolterstorff, 1914
            - *Notophthalmus (Notophthalmus) viridescens piaropicola* (Schwartz & Duellman 1952)
            - *Notophthalmus (Notophthalmus) viridescens viridescens* (Rafinesque, 1820)
      - ***Rafinus*** nov.
        - ***Notophthalmus*** *(Rafinus) meridionalis* (Cope, 1880)
            - *Notophthalmus (Rafinus) meridionalis kallerti* (Wolterstorff 1930)
            - *Notophthalmus (Rafinus) meridionalis meridionalis* (Cope, 1880)
    - ***Taricha*** Gray **1850**
      - **Incertae sedis**
        - † ***Taricha*** *lindoei* Naylor 1979
        - † ***Taricha*** *miocenica* Tihen 1974
        - † ***Taricha*** *oligocenica* (Van Frank, 1955)
      - ***Taricha*** Gray, 1850
        - ***Taricha*** *(Taricha) granulosa* (Skilton, 1849)
        - ***Taricha*** *(Taricha) sierrae* (Twitty 1942)
        - ***Taricha*** *(Taricha) torosa* (Rathke, 1833)
      - ***Twittya*** nov.
        - ***Taricha*** *(Twittya) rivularis* (Twitty 1935)
- *PLEURODELINI* **Tschudi, 1838**
    - **Incertae sedis**
        - † *Triturus schmidtlerianus* Herre & Lunau 1950
    - † ***Brachycormus*** **Meyer**, 1860
        - † ***Brachycormus*** *noachicus* (Goldfuss, 1831)
    - † ***Chelotriton*** **Pomel** 1853
        - † ***Chelotriton*** *ogygius* (Goldfuss, 1831)
        - † ***Chelotriton*** *paradoxus* Pomel 1853
        - † ***Chelotriton*** *pliocenicus* Bailon 1989
        - † ***Chelotriton*** *robustus* Westphal, 1979

Table 5. – (continued 3).

sF	T	sT	iT	G	sG	SS	S	E	sS
				Echinotriton Nussbaum & Brodie, 1982					
							Echinotriton andersoni (Boulenger, 1892)		
							Echinotriton chinhaiensis (Chang, 1932)		
				† ***Palaeopleurodeles*** Herre, 1941					
							† *Palaeopleurodeles hauffi* Herre, 1941		
				Pleurodeles Michahelles, 1830					
							Pleurodeles nebulosus (Guichenot, 1850)		
							Pleurodeles poireti (Gervais, 1835)		
							Pleurodeles waltl Michahelles, 1830		
				Tylototriton Anderson, 1871					
					Incertae sedis				
							† *Tylototriton weigelti* Herre, 1935		
					Tylototriton Anderson, 1871				
							Tylototriton (Tylototriton) kweichowensis Fang & Chang, 1932		
							Tylototriton (Tylototriton) shanjing Nussbaum, Brodie & Yang, 1995		
							Tylototriton (Tylototriton) taliangensis Liu, 1950		
							Tylototriton (Tylototriton) verrucosus Anderson, 1871		
					Yaotriton nov.				
							Tylototriton (Yaotriton) asperrimus Unterstein, 1930		
							Tylototriton (Yaotriton) hainanensis Fei, Ye & Yang, 1984		
							Tylototriton (Yaotriton) vietnamensis Bohme, Schöttler, Nguyen & Köhler, 2005		
							Tylototriton (Yaotriton) wenxianensis (Fei, Ye & Yang, 1984)		
SALAMANDRINAE Goldfuss, 1820									
	CHIOGLOSSINI nov								
				Chioglossa Bocage, 1864					
							Chioglossa lusitanica Bocage, 1864		
									Chioglossa lusitanica longipes Arntzen, Groenenberg, Alexandrino, Ferrand & Sequeira, 2007
									Chioglossa lusitanica lusitanica Bocage, 1864
							† *Chioglossa meini* Estes & Hoffstetter, 1976		
				Mertensiella Wolterstorff, 1925					
							Mertensiella caucasica (Waga, 1876)		
							† *Mertensiella mera* Hodrova, 1984		
	SALAMANDRINI Goldfuss, 1820								
				Lyciasalamandra Veith & Steinfartz, 2004					
							Lyciasalamandra antalyana (Basoglu & Baran, 1976)		
							Lyciasalamandra atifi (Basoglu, 1967)		
							Lyciasalamandra billae (Franzen & Klewen, 1987)		
							Lyciasalamandra fazilae (Basoglu & Atatür, 1974)		
							Lyciasalamandra flavimembris (Mutz & Steinfartz, 1995)		
							Lyciasalamandra helverseni (Pieper, 1963)		
							Lyciasalamandra luschani (Steindachner, 1891)		
									Lyciasalamandra luschani basoglui (Baran & Atatür, 1980)
									Lyciasalamandra luschani finikensis (Basoglu & Atatür, 1975)
									Lyciasalamandra luschani luschani (Steindachner, 1891)
				† ***Megalotriton*** Zittel, 1890					
							† *Megalotriton filholi* Zittel, 1890		
				Salamandra Laurenti, 1768					
					Incertae sedis				
							† *Salamandra goussardiana* Lartet, 1851		
							† *Salamandra sansaniensis* Lartet, 1851		
					Algandra nov				
							Salamandra (Algandra) algira Bedriaga, 1883		
									Salamandra (Algandra) algira algira Bedriaga, 1883
									Salamandra (Algandra) algira spelaea Escoriza & Comas, 2007
							Salamandra (Algandra) tingitana Donaire, Barroso & Bogaerts, 2003		

Table 5. – (continued 4).

sF	T	sT	iT	G	sG	SS	S	E	sS
					Alpandra nov.				
							Salamandra (Alpandra) atra Laurenti, 1768		
									Salamandra (Alpandra) atra atra Laurenti, 1768
									Salamandra (Alpandra) atra pasubiensis Bonato & Steinfartz, 2005
									Salamandra (Alpandra) atra prenjensis Miksic, 1969
							Salamandra (Alpandra) aurorae Trevisan, 1982		
					Corsandra nov.				
							Salamandra (Corsandra) corsica Savi, 1838		
					Mimandra nov.				
							Salamandra (Mimandra) lanzai Nascetti, Andreone, Capula & Bullini, 1988		
					Oriandra nov.				
							Salamandra (Oriandra) infraimmaculata Martens, 1885		
									Salamandra (Oriandra) infraimmaculata infraimmaculata Martens, 1885
									Salamandra (Oriandra) infraimmaculata orientalis Wolterstorff, 1925
									Salamandra (Oriandra) infraimmaculata semenovi Nesterov, 1916
					Salamandra Laurenti, 1768				
							Salamandra (Salamandra) almanzoris Müller & Hellmich, 1935		
							Salamandra (Salamandra) longirostris Joger & Steinfartz, 1994		
							Salamandra (Salamandra) salamandra (Linnaeus, 1758)		
								crespoi Malkmus, 1983	
									Salamandra (Salamandra) salamandra (crespoi) crespoi Malkmus, 1983
									Salamandra (Salamandra) salamandra (crespoi) morenica Joger & Steinfartz, 1994
								fastuosa Schreiber, 1912	
									Salamandra (Salamandra) salamandra (fastuosa) alfredschmidti Köhler & Steinfartz, 2006
									Salamandra (Salamandra) salamandra (fastuosa) bernardezi Wolterstorff, 1928
									Salamandra (Salamandra) salamandra (fastuosa) fastuosa Schreiber, 1912
									Salamandra (Salamandra) salamandra (fastuosa) gigliolii Eiselt & Lanza, 1956
								salamandra (Linnaeus, 1758)	
									Salamandra (Salamandra) salamandra (salamandra) bejarae Wolterstorff, 1934
									Salamandra (Salamandra) salamandra (salamandra) beschkovi Obst, 1981
									Salamandra (Salamandra) salamandra (salamandra) gallaica Seoane, 1885
									Salamandra (Salamandra) salamandra (salamandra) salamandra (Linnaeus, 1758)
									Salamandra (Salamandra) salamandra (salamandra) terrestris Bonnaterre, 1789
									Salamandra (Salamandra) salamandra (salamandra) werneri Sochurek & Gayda, 1941
SALAMANDRININAE Fitzinger, 1843									
				† *Archaeotriton* Meyer, 1860					
							† *Archaeotriton basalticus* (Meyer, 1859)		
				Salamandrina Fitzinger, 1826					
							Salamandrina perspicillata (Savi, 1821)		
							Salamandrina terdigitata (Bonnaterre, 1789)		

The ergotaxonomy here presented includes 253 situations of hypotaxy as defined above (see table 6), which are distributed as follows in the four categories distinguished above: (1) 52 cases (20.6 %) of monohypotaxy, (2) 25 cases (9.9 %) of diplohypotaxy, (3) 17 cases (6.7 %) of polyhypotaxy, and (4) 159 cases (62.8 %) of anhypotaxy, including 99 species without subspecies and 60 subspecies. In this case, as we used a finely divided nomenclatural hierarchy to express this taxonomy, all cases of polyhypotaxy can be considered to express unresolved polytomies. As they amount for less than 7 % of cases, this suggests that for this family of salamanders the available data support rather well resolved relationships between taxa. This does not mean at all that this ergotaxonomy is "final", especially as new taxa certainly await discovery and description.

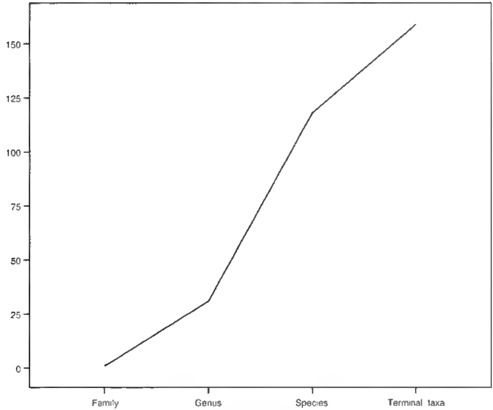


Fig. 2. Number of taxa at the four major ranks family, genus, species and "terminal taxon" (i.e., either species or subspecies) recognized in the ergotaxonomy of the *SALAMANDRIDAE* here adopted.

To express this rather detailed hierarchical ergotaxonomy, less nomina then taxa are necessary, as expressed by the nomenclatural parsimony ratio defined above. In the family series, only 8 nomina (including 4 new ones, i.e., 50.0 %) are needed for 13 taxa (NPR 61.5 %). In the genus-series, 44 nomina (including 11 new ones, i.e. 25.0 %) are needed for 54 taxa (NPR 81.5 %). In the species-series, 148 nomina (without any new one) are needed for 186 taxa (NPR 79.0 %).

The 11 genus series nomina created here have from 6 to 9 letters (mean 8.0, median 8.0). This results in a decrease in the mean (10.3 vs. 11.6) and median (10.0 vs. 11.0) numbers of letters of the generic nomina of the whole family (see above), which however is not significant, although almost so, compared to the previous situation (Mann-Whitney *U* test, *U* = 628.5, *P* = 0.052). This number remains significantly higher than in the *RANIDAE* (Mann-Whitney *U* test, *U* = 497.5, *P* = 0.002). This is because very long nomina created previously in the *SALAMANDRIDAE* still remain (and will have to remain) in use in this family. However, a strong change in the historical trend in the the length of nomina over time since 1758 is now evident

Table 6. – Number of cases of each category of hypotaxy (see text for explanation) represented at each rank in the ergotaxonomy of the *SALAMANDRIDAE* here proposed. Ranks, F, familia, sF, subfamilia, T, tribus, sT, subtribus, iT, infratribus, G, genus, sG, subgenus; SS, supraspecies, S, species, E, exerge; sS, subspecies.

Category of hypotaxy	F	sF	T	sT	iT	G	sG	SS	S	E	sS	Total
Monohypotaxy	0	1	3	1	1	22	22	2	0	0	0	52
Diplohypotaxy	0	2	1	0	0	8	0	0	13	1	0	25
Polyhypotaxy	1	0	0	1	2	1	1	1	6	4	0	17
Anhypotaxy	0	0	0	0	0	0	0	0	99	0	60	159
Total	1	3	4	2	3	31	23	3	118	5	60	253

(fig. 1). We suggest a similar voluntary limitation in the length and complexity of generic nomina would be beneficial in all other amphibian families, and probably also over the whole of zootaxonomy. Non-taxonomists are looking at taxonomists and their works, and they often make negative comments on the "barbarian" nomina often given to taxa by the latter.

As mentioned above, the taxonomic impediment is still quite important in almost all groups of amphibians. Although long studied, the taxonomy of the salamanders of the family *SALAMANDRIDAE* is still not stabilized and should not be considered so. In the future years and decades, we will certainly witness many descriptions of new species, subspecies and taxa at various levels above species, changes of ranks for already recognized taxa (e.g., subspecies elevated to species rank) and "resurrection" of once synonymized nomina. We think that this trend will allow a better protection and conservation of these endangered organisms. At the beginning of the century of extinctions (DUBOIS, 2003*a*), the role of taxonomy is an important one. As we have seen, legislative texts that have consequences on the conservation of amphibian populations or habitats are highly dependent on the existence of formally named taxa, which can be placed on "official lists". Therefore, as soon as they have data, even preliminary, pointing to the distinctness or uniqueness of populations or groups, taxonomists should seriously consider recognizing the latter as formal taxa and naming them. Refraining too long from recognizing new taxa because of "uncertainties" is not doing a service to the study and conservation of biodiversity. It is better to have to synonymize a nomen when new data suggest that the taxon for which it was coined was unwarranted than being unable to protect an interesting or unique population because it does not bear a special nomen. We live at a special period of the history of taxonomy when "taxonomic cramps" amount to genuine errors.

ACKNOWLEDGEMENTS

We are grateful to the many persons who helped for the realisation of this study. Serge Bogaerts, Jean-Claude Concaro, Arnaud Jamin, Emmanuel Jelsch, Nicolas Lopez, François Maillet and Max Sparreboom provided unpublished information on salamanders in captivity. Michel Breuil, Pierre-Andre Crochet, Veronique Helfer, Spartak Litvinchuk and Fabrice Meral provided unpublished data on salamanders or on nomina. Roger Bour, Myrianne Brival, Britta and Heinz Grillitsch, Andrea Kourgli

and Victoire Koyamba provided information and/or helped in bibliographic research. Roger Bour prepared the tables for print. Annemarie Ohler made very constructive comments on the manuscript and helped for translations, calculations, tables and graphs.

LITERATURE CITED

Anonymous [International Commission on Zoological Nomenclature], 1925. - Opinions rendered by the International Commission on Zoological Nomenclature. Opinion 89. Suspension of the Rules in the case of Gronow 1763, Commerson 1803, Gesellschaft Schauplatz 1775 to 1781, Catesby 1771, Browne 1789, Valmont de Bomare 1768 to 1775. *Smithsonian miscellaneous Collections*, **73** (3): 27-33.

--- [International Commission on Zoological Nomenclature], 1929. - Opinions rendered by the International Commission on Zoological Nomenclature. Opinion 105. Dybowski's (1926) names of Crustacea suppressed. *Smithsonian miscellaneous Collections*, **73** (6): 1-3.

----- [Systematics Agenda 2000], 1994. - *Charting the biosphere: a global initiative to discover, describe and classify the world's species. Technical report.* New York, American Museum of Natural History, American Society of Plant Taxonomy, Society of Systematic Biologists and the Willi Hennig Society: 1-34.

----- [International Commission on Zoological Nomenclature], 1997. - Opinion 1873. Hemidactylium Hallowell, 1856 (Amphibia, Caudata): conserved. *Bulletin of zoological Nomenclature*, **54**: 140-141.

----- [International Commission on Zoological Nomenclature], 1999. - *International code of zoological nomenclature*. Fourth edition. London, International Trust for zoological Nomenclature: i-xxix + 1-306.

----- [International Commission on Zoological Nomenclature], 2005. - Opinion 2104 (Case 3226). Lacepède, B. G. E. de la V., 1788, *Histoire naturelle des Quadrupèdes Ovipares*: rejected as a non-binominal work. *Bulletin of zoological Nomenclature*, **62** (1): 55.

----- [International Commission on Zoological Nomenclature], 2008. - Proposed amendment of the *International Code of Zoological Nomenclature* to expand and refine methods of publication. *Zootaxa*, **1908**: 57-67.

Attobello, G., 1926. - Forme locali. Vertebrati del Molise e dell'Abruzzo. *Annuar. Ist. tec. L. Pilla*, Campobasso, **1925-1926**: 1-26. [Not seen]

Anderson, J., 1871. - Description of a new genus of newts from western Yunan. *Proceedings of the zoological Society of London*, **1871**: 423-425.

Andreone, F., 1990. - *Variabilità morfologica e riproduttiva in popolazioni italiane di* Triturus alpestris *(Laurenti, 1768) (Amphibia, Salamandridae)*. Thesis, Università degli Studi di Bologna e sedi consorziate (Università di Ferrara, Modena, Parma): 1-331.

Arntzen, J. W. & Thorpe, R. S., 1999. - Italian crested newts (*Triturus carnifex*) in the basin of Geneva: distribution and genetic interactions with autochthonous species. *Herpetologica*, **55** (4): 423-433.

Ashlock, P. D., 1971. - Monophyly and associated terms. *Systematic Zoology*, **20**: 63-69.

---- 1985. - A revision of the *Bergidea* group: a problem in classification and biogeography. *Journal of the Kansas entomological Society*, **27**: 675-688.

Assmann, T. & Habel, J. C., 2009. - *Survival on changing climate: phylogeography and conservation of relict species*. Heidelberg, Springer Verlag: in press.

Avise, J. C., 2000. - *Phylogeography: the history and formation of species*. Cambridge, MA., Harvard University Press: 1-447.

Babik, W., Branicki, W., Crnobrnja-Isailovic, J., Cogalniceanu, D., Sas, I., Olgun, K., Poyarkov, N. A., Garcia-Paris, M. & Arntzen, J. W., 2005. - Phylogeography of two European newt species: discordance between mtDNA and morphology. *Molecular Ecology*, **14**: 2475-2491.

Bataillon, E., 1927. - Les croisements chez les Urodèles et l'androgenèse hybride. *Comptes rendus hebdomadaires des Séances et Mémoires de la Société de Biologie et de ses Filiales*, **97** (2): 1715-1717.

BATAILLON, E. & TCHOU SU, 1932. Croisements en retour (2^{e} génération) entre une femelle hybride d'Urodèle et les mâles des deux types parentaux. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences*, **195**: 449-452.

BEDRIAGA, J. v., 1883. – Beiträge zur Kenntniss der Amphibien und Reptilien der Fauna von Corsika. *Archiv für Naturgeschichte*, **49** (1): 124-273, pl. 3-5.

BELL, T., 1839. – *A history of British Reptiles*. London, John Van Voorst: i-xxiv + 1-142.

BERNARDI, G., 1980. - Les catégories taxonomiques de la systématique évolutive. *Mémoires de la Société zoologique de France*, **40**: 373-425.

BLANCHARD, R., 1879. Société zoologique de France. Séance du 18 février 1879. *Revue internationale des Sciences*, **3**: 275-276.

BOCAGE, J. V. B. DU, 1864. Notice sur un Batracien nouveau du Portugal (*Chioglossa lusitanica*, nob.). *Proceedings of the zoological Society of London*, **1864**: 264-265, pl. 21.

BOCQUET, C., 1976. Les problèmes de l'espèce chez quelques Crustacés: le genre *Tisbe* (Copépodes Harpacticoïdes) et le complexe *Jaera albifrons* (Isopodes Asellotes). *Mémoires de la Société zoologique de France*, **38**: 307-340.

BODDAERT, P., 1770*a*. – *II. Over den Gevlakten Klipvisch. De* Chaetodonte argo. Amsterdam, Kornelis van Tongerlo: [i-iv] + 1-44, 1 pl.

----- 1770*b*. *III. Over de Kraakbeenige Schildpad. De* Testudine cartilaginea. Amsterdam, Kornelis van Tongerlo: [i-iv] + 1-40, 1 pl.

----- 1772*a*. *IV. Over den Twee-Koleurigen Kikvorsch. De* Rana bicolore. Amsterdam, Magerus: 1-48, 3 pl.

----- 1772*b*. *V. Over den Tweedoornigen Klipvisch. De* Chaetodonte diacantho. Amsterdam, Magérus: 1-44, 1 pl.

BOETTGER, O., 1879. Amphibien aus Südportugal. Aufzählung der von Freih. H. v. Maltzan-Federow März und April 1879 in Alemtejo und im Königreich Algarve gesammelten Reptilien und Batrachier. *Zeitschrift für die gesammten Naturwissenschaften*, Berlin, **52** (3): 497-534.

BOIE, H., 1826. – Merkmale einiger japanischer Lurche. *Isis von Oken*, **1826** (1): 203-216.

BOLKAY, S. J., 1927. – Materialen zu einer vergleichenden Morphologie der Carpal- und Tarsalelemente der Unterfamilie Salamandrinae. *Glasnik Zemaljskog Muzeja u Bosni i Hercegovini*, **39**: 59-67, pl. 1-3.

BONATO, L. & STEINFARTZ, S., 2005. Evolution of the melanistic colour in the Alpine salamander *Salamandra atra* as revealed by a new subspecies from the Venetian Prealps. *Italian Journal of Zoology*, **72**: 253-260.

BONNATERRE, Abbé, 1789. *Tableau encyclopédique et méthodique des trois règnes de la nature. Erpétologie*. Paris, Panckoucke: i-xxviii + 1-71, 26 pl.

BOULENGER, G. A., 1880. Sur une forme intéressante de Triton provenant de Moldavie et observations sur le genre *Pelonectes* Lataste. *Bulletin de la Société zoologique de France*, **5**: 37-40.

----- 1882. *Catalogue of the Batrachia Gradientia s. Caudata in the collection of the British Museum*. Second edition. London, Taylor & Francis: i-ix + 1-127, pl. 1-9.

----- 1905. Description of a new newt from Yunnan. *Proceedings of the zoological Society of London*, **1905**: 277-278, pl. 17.

BOUR, R., CHEYLAN, M., CROCHET, P. A., GENIEZ, P., GUYÉTANT, R., HAFFNER, P., INEICH, I., NAULLEAU, G., OHLER, A. & LESCURE, J., 2008. Liste taxinomique actualisée des Amphibiens et Reptiles de France. *Bulletin de la Société herpétologique de France*, **126**: 37-43.

BOUR, R. & DUBOIS, A., 1984. Nomenclatural availability of *Testudo coriacea* Vandelli, 1761: a case against a rigid application of the Rules to old, well-known zoological words. *Journal of Herpetology*, **17**: 356-361.

BOURRET, R., 1934. Notes herpétologiques sur l'Indochine française. VII. Une salamandre nouvelle vivant au Tonkin. *Bulletin général de l'Instruction publique*, **14** (1934-1935), (4) (Décembre): 83-84 [11-12], 1 pl.

BREUIL, M., 1983. *Variabilité génétique de quelques populations de Triton alpestre (*Triturus alpestris*) (Amphibia Caudata, Salamandridae) des Alpes et des Apennins*. Diplôme d'Études Approfondies. Orsay, Université de Paris-Sud: [i-ii] + 1-33.

----- 1986. *Biologie et différenciation génétique des populations du Triton alpestre (*Triturus alpestris*) (Amphibia Caudata) dans le Sud-Est de la France et en Italie*. Thesis. Orsay, Université de Paris-Sud: i-xiii + 1-192.

Breuil, M. & Guillaume, C.-P., 1985. – Etude électrophorétique de quelques populations de Tritons alpestres néoteniques (*Triturus alpestris*, Amphibia, Caudata, Salamandridae) du sud de la Yougoslavie. *Bulletin de la Société zoologique de France*, **109** (4): 377-389.

Brongniart, A., 1800. – Essai d'une classification naturelle des reptiles. I^{ère} partie. Etablissement des ordres. *Bulletin des Sciences, par la Société philomatique*, **2** (35): 81-82.

Brummitt, R. K., 1997. – Taxonomy versus cladonomy, a fundamental controversy in biological systematics. *Taxon*, **46**: 723-734.

Bucci-Innocenti, S., Ragghianti, M. & Mancino, G., 1983. – Investigations of karyology and hybrids in *Triturus boscai* and *T. vittatus*, with a reinterpretation of the species groups within *Triturus* (Caudata: Salamandridae). *Copeia*, **1983** (3): 662-672.

Caccone, A., Milinkovitch, M. C., Sbordoni, V. & Powell, J. R., 1994. – Molecular biogeography: using the Corsica-Sardinia microplate disjunction to calibrate mitochondrial rDNA evolutionary rates in mountain newts (*Euproctus*). *Journal of evolutionary Biology*, **7**: 227-245.

----- 1997. – Mitochondrial DNA rates and biogeography in European newts (genus *Euproctus*). *Systematic Biology*, **46** (1): 126-144.

Cahet, P., 1963. – A propos de *Salamandra salamandra almanzoris* Müller et Hellmich. *Vie & Milieu*, **14**: 651-654.

Carranza, S. & Amat, F., 2005. – Taxonomy, biogeography and evolution of *Euproctus* (Amphibia, salamandridae), with the resurrection of the genus *Calotriton* and the description of a new endemic species from the Iberian Peninsula. *Zoological Journal of the Linnean Society*, **145**: 555-582.

Chan, L. M., Zamudio, K. R. & Wake, D. B., 2001. – Relationships of the salamandrid genera *Paramesotriton*, *Pachytriton*, and *Cynops* based on mitochondrial DNA sequences. *Copeia*, **2001** (4): 997-1009.

Chang, M. L. Y., 1933. – On the salamanders of Chekiang. *Contributions from the biological Laboratory of the Science Society of China, Zoological Series*, **9** (8): 305-328.

----- 1935. – Note preliminaire sur la classification des Salamandres d'Asie orientale. *Bulletin de la Société zoologique de France*, **60**: 424-427.

----- 1936. – *Contribution a l'etude morphologique, biologique et systematique des Amphibiens Urodeles de la Chine*. Paris, Picart: 1-156.

Cirović, R., Radović, D. & Vukov, T. D., 2008. – Breeding site traits of European newts (*T. macedonicus*, *Lissotriton vulgaris*, and *Mesotriton alpestris*: Salamandridae) in the Montenegrin Karst region. *Archives of biological Sciences of Belgrade*, **60** (3): 459-468.

Cope, E. D., 1862. – Notes upon some Reptiles of the Old World. *Proceedings of the Academy of natural Sciences of Philadelphia*, **14**: 337-344.

----- 1880. – On the zoological position of Texas. *Bulletin of the United States national Museum*, **17**: 1-51. [Not seen]

Cuenot, L. & Tetry, A., 1951. – *L'evolution biologique. Les faits, les incertitudes*. Masson, Paris: i-ix + 1-588.

David, A., 1875. – *Journal de mon troisième voyage d'exploration dans l'Empire Chinois*. 2. Paris, Hachette: [i-iii] + 1-348, 1 map.

De Blainville, H., 1816. – Prodrome d'une nouvelle distribution systematique du regne animal. *Bulletin des Sciences de la Societe philomatique de Paris*, juillet 1816: "105-112" [actually 113-120] + 121-124.

De L'Isle du Dreneuf, A., 1862. – Notice zoologique sur un nouveau Batracien Urodele de France. *Annales des Sciences naturelles*, (4), *Zoologie*, **17**: 363-371, pl. 12.

De la Cepede, [B. G. E.], 1788a. – *Histoire naturelle des quadrupedes ovipares et des serpens*. Tome premier. 16 cm. Paris, Hôtel de Thou: 1-60 + 1-359, pl. 1-12.

----- 1788b. – *Histoire naturelle des quadrupedes ovipares et des serpens*. Tome second. 16 cm. Paris, Hôtel de Thou: [i-iv] + 1-464, pl. 1-15.

De Queiroz, K. & Gauthier, J., 1990. – Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Zoology*, **39** (4): 307-322.

----- 1994. – Toward a phylogenetic system of biological nomenclature. *Trends in Ecology & Evolution*, **9**: 27-31.

DELY, O. G., 1960. – Examen du Triton alpestre (*Triturus alpestris* Laurenti) spécialement en vue des populations de la Hongrie et des Carpathes. *Acta zoologica Academiae Scientiarum Hungaricae*, **5** (3-4): 255-315, 4 pl.

DOMINGUEZ, F. & WHEELER, Q. D., 1997. – Taxonomic stability is ignorance. *Cladistics*, **13**: 367-372.

DONAIRE BARROSO, D. & BOGAERTS, S., 2003. – A new subspecies of *Salamandra algira* Bedriaga, 1883 from northern Morocco. *Podarcis*, **4** (3): 84-100.

DUBOIS, A., 1977. – Les problèmes de l'espèce chez les Amphibiens Anoures. *Mémoires de la Société zoologique de France*, **39**: 161-284.

---- 1981. – Liste des genres et sous-genres nominaux de Ranoidea (Amphibiens, Anoures) du monde, avec identification de leurs especes-types: consequences nomenclaturales. *Monitore zoologico italiano*, (n.s.), **15**, suppl.: 225-284.

---- 1982. – Les notions de genre, sous-genre et groupe d'espèces en zoologie a la lumiere de la systématique évolutive. *Monitore zoologico italiano*, (n. s.), **16**: 9-65.

---- 1985. – Miscellanea nomenclatorica batrachologica (VII). *Alytes*, **4** (2): 61-78.

---- 1987*a*. – Miscellanea taxinomica batrachologica (I). *Alytes*, "1986", **5** (1-2): 7-95.

---- 1987*b*. – Reviews and comments. *Amphibian species of the world. A taxonomic and geographical reference*.1st ed. D. R. Frost (ed.). 1985. *Copeia*, **1987**: 830-833.

---- 1987*c*. – Living amphibians of the world: a first step towards a comprehensive checklist. *Alytes*, **5** (3): 99-149.

---- 1987*d*. – Again on the nomenclature of frogs. *Alytes*, **6** (1-2): 27-55.

---- 1988*a*. – Some comments on the genus concept in zoology. *Monitore zoologico italiano*, (n. s.), **22**: 27-44.

---- 1988*b*. – The genus in zoology: a contribution to the theory of evolutionary systematics. *Mémoires du Muséum national d'Histoire naturelle*, (A), **140**: 1-123.

---- 1991. – Nomenclature of parthenogenetic, gynogenetic and "hybridogenetic" vertebrate taxons: new proposals. *Alytes*, "1989-1990", **8**: 61-74.

---- 1992. – Notes sur la classification des Ranidae (Amphibiens, Anoures). *Bulletin mensuel de la Société linnéenne de Lyon*, **61** (10): 305-352.

---- 1994. – Comment on the proposed conservation of Hemidactylium Hallowell, 1856 (Amphibia, Caudata). *Bulletin of zoological Nomenclature*, **51**: 264-265.

--- 1997. – An evolutionary biologist's view on the science of biology. *Alytes*, **15**: 133-136.

---- 1998*a*. – List of European species of amphibians and reptiles: will we soon be reaching "stability"? *Amphibia-Reptilia*, **19** (1): 1-28.

---- 1998*b*. – Mapping European amphibians and reptiles: collective inquiry and scientific methodology. *Alytes*, **15** (4): 176-204.

---- 2000. – Synonymies and related lists in zoology: general proposals, with examples in herpetology. *Dumerilia*, **4** (2): 33-98.

---- 2003*a*. – The relationships between taxonomy and conservation biology in the century of extinctions. *Comptes rendus Biologies*, **326** (suppl. 1): S9-S21.

---- 2003*b*. – Should internet sites be mentioned in the bibliographies of scientific publications? *Alytes*, **21** (1-2): 1-2.

---- 2004*a*. – *Alytes*, a different journal. *Alytes*, **21** (3-4): 105-110.

---- 2004*b*. – Developmental pathway, speciation and supraspecific taxonomy in amphibians. 2. Developmental pathway, hybridizability and generic taxonomy. *Alytes*, **22** (1-2): 38-52.

---- 2005*a*. – Propositions pour l'incorporation des nomina de taxons de rang superieur dans le *Code international de nomenclature zoologique*. *In*: A. DUBOIS, O. PONCY, V. MALECOT & N. LÉGER (ed.), *Comment nommer les taxons de rang supérieur en zoologie et en botanique?*, *Biosystema*, **23**: 73-96.

---- 2005*b*. – Proposed Rules for the incorporation of nomina of higher-ranked zoological taxa in the *International Code of Zoological Nomenclature*. 1. Some general questions, concepts and terms of biological nomenclature. *Zoosystema*, **27** (2), 365–426.

---- 2005*c*. – *Amphibia Mundi*. 1.1. An ergotaxonomy of recent amphibians. *Alytes*, **23** (1-2): 1-24.

---- 2005*d*. – Proposals for the incorporation of nomina of higher-ranked taxa into the Code. *Bulletin of zoological Nomenclature*, **62** (4): 200-209.

---- 2006*a*. – Proposed Rules for the incorporation of nomina of higher-ranked zoological taxa in the *International Code of Zoological Nomenclature*. 2. The proposed Rules and their rationale. *Zoosystema*, **28** (1): 165-258.

----- 2006*b*. – New proposals for naming lower-ranked taxa within the frame of the *International Code of Zoological Nomenclature*. *Comptes rendus Biologies*, **329** (10): 823-840.

----- 2006*c*. – Naming taxa from cladograms: a cautionary tale. *Molecular Phylogenetics & Evolution*, **42**: 317-330.

----- 2007*a*. – Phylogeny, taxonomy and nomenclature: the problem of taxonomic categories and of nomenclatural ranks. *Zootaxa*, **1519**: 27-68.

----- 2007*b*. – Genitives of species and subspecies nomina derived from personal names should not be emended. *Zootaxa*, **1550**: 49-68.

----- 2007*c*. – Naming taxa from cladograms: some confusions, misleading statements, and necessary clarifications. *Cladistics*, **23**: 390-402.

----- 2008*a*. – A partial but radical solution to the problem of nomenclatural taxonomic inflation and synonymy load. *Biological Journal of the Linnean Society*, **93**: 857-863.

----- 2008*b*. – Drôles d'espèces. Hybridation, perturbations de la meiose et spéciation dans le règne animal: quelques points délicats de terminologie, d'eidonomie et de nomenclature. *In*: D. Prat, A. Raynal-Roques & A. Roguenant (ed.), *Peut-on classer le vivant? Linné et la systématique aujourd'hui*, Paris, Belin: 169-202.

----- 2008*c*. – Le *Code international de nomenclature zoologique*: présentation, philosophie, règles majeures, problemes actuels. *In*: D. Prat, A. Raynal-Roques & A. Roguenant (ed.), *Peut-on classer le vivant? Linné et la systématique aujourd'hui*, Paris, Belin: 355-402.

----- 2008*d*. – Phylogenetic hypotheses, taxa and nomina in zoology. *Zootaxa*, **1950**: 51-86.

----- 2009*a*. – Miscellanea nomenclatorica batrachologica. 20. Class-series nomina are nouns in the nominative plural: Terrarana Hedges, Duellman & Heinicke, 2008 must be emended. *Alytes*, **26** (1-4): 167-175.

----- 2009*b*. – Qu'est-ce qu'une espèce animale? *Annales de la Société entomologique de France*, in press.

Dubois, A. & Breuil, M., 1983. – Découverte de *Triturus alpestris* (Laurenti, 1768) en Calabre (sud de l'Italie). *Alytes*, **2** (1): 9-18.

Dubois, A. & Günther, R., 1982. – Klepton and synklepton: two new evolutionary systematics categories in zoology. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie & Biologie der Tiere*, **109**: 290-305.

Dubois, A. & Ohler, A., 1995. – Frogs of the subgenus *Pelophylax* (Amphibia, Anura, genus *Rana*): a catalogue of available and valid scientific names, with comments on name-bearing types, complete synonymies, proposed common names, and maps showing all type localities. *Zoologica Poloniae*, "1994", **39** (3-4): 139-204.

----- 1997. – Early scientific names of Amphibia Anura. I. Introduction. *Bulletin du Muséum national d'Histoire naturelle*, "1996", (4), **18** (3-4): 297-320.

----- 2009. – Nomina Amphibiorum. 1. The status of the amphibian nomina created by Merrem (1820) and Ritgen (1828). *Zootaxa*, accepted pending modifications.

Dugès, A., 1852. – Recherches zoologiques sur les Urodèles de France. *Annales des Sciences naturelles*, (3), *Zoologie*, **17**: 253-272 + [i], pl. 1.

Duméril, A. M. C., 1806. – *Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques*. Paris, Allais: i-xxxiii + 1-544.

Dupuis, C., 1979. – Permanence et actualité de la systematique: la "systématique phylogenetique" de W. Hennig (historique, discussion, choix de références). *Cahiers des Naturalistes, Bulletin des Naturalistes parisiens*, (n.s.), "1978", **34** (1): 1-69.

Dybowski, B., 1926. – Synoptisches Verzeichnis mit kurzer Besprechung der Gattungen und Arten dieser Abteilung der Baikalflohkrebse. *Bulletin international de l'Académie polonaise des Sciences et des Lettres, Classe des Sciences mathématiques et naturelles*, (B), *Sciences naturelles*, Cracovie, **1926**: 1-77.

Eiselt, J., 1958. – Der Feuersalamander *Salamandra salamandra* (L.). Beiträge zu einer taxonomischen Synthese. *Abhandlungen und Berichte für Naturkunde und Vorgeschichte*, Magdeburg, **10** (6): 77-154, 1 pl.

Escoriza, D. & Comas, M. del Mar, 2007. – Description of a new subspecies of *Salamandra algira* Bedriaga, 1883 (Amphibia: Salamandridae) from the Beni Snassen massif (Northeast Morocco). *Salamandra*, **43** (2): 77-90.

Escoriza, D., Comas, M. M., Donaire, D. & Carranza, S., 2006. Rediscovery of *Salamandra algira* Bedriaga, 1833 from the Beni Snassen massif (Morocco) and phylogenetic relationships of North African *Salamandra*. *Amphibia-Reptilia*, **27** (3). 448-455

Estes, R., 1981. Gymnophiona, Caudata. In: P. Wellnhofer (ed.), *Handbuch der Palaoherpetologie*, **2** (2), Stuttgart, Gustav Fischer: i-xv + 1-115

Fang, Z. & Zhao, E., 1992. – A systematic review of Chinese toads *Bufo* (Anura, Bufonidae). *In*: Y. Jiang (ed.), *Collected papers on herpetology*, Chengdu, Sichuan Publishing House of Science and Technology. 77-88. [In Chinese].

Fatio, V., 1872. *Faune des Vertébres de la Suisse*. **3.** *Histoire naturelle des Reptiles et des Batraciens*. Genève & Bâle, Georg: i-iii + 1-603, pl. 1-5

Fei, L. (ed.), 1999. - *Atlas of amphibians of China*. Zhengzhou (China), Henan Press of Science and Technology: [i-ii] + 1-432. [In Chinese.]

Fei, L., Hu, S., Ye, C. & Huang, Y., 2006. *Fauna Sinica. Amphibia*. **1.** *General accounts of Amphibia Gymnophiona and Urodela*. Beijing, Science Press. [i-ix] + i-viii + 1-471, pl. 1-16

Fei, L., Ye, C. & Huang, Y., 1990. *Key to Chinese Amphibia*. Chongqing, Editions of Sciences and Techniques. [i-iv] + 1-2 + 1-364. [In Chinese]

Fei, L., Ye, C., Huang, Y., Jiang, J. & Xie, F., 2005. *An illustrated key to Chinese amphibians*. Sichuan Publishing Group, Sichuan Publishing House of Science & Technology, i-v + 1-340, pl. 1-12. [In Chinese]

Ferrier, V. & Beetschen, J.-C., 1973. Etude des chromosomes de *Tylototriton verrucosus* Anderson et de l'hybride viable *Pleurodeles waltlii* ♀ × *Tylototriton verrucosus* ♂ (Amphibiens Urodèles, Salamandridae). *Chromosoma*, **42** (1). 57-69.

Ferrier, V., Beetschen, J.-C. & Jaylet, A., 1971. Réalisation d'un hybride intergénérique viable entre deux Amphibiens Urodèles européen et asiatique (*Pleurodeles waltlii* ♀ × *Tylototriton verrucosus* ♂, Salamandridae). *Comptes rendus des Séances de l'Academie des Sciences de Paris*, (D), **272**: 3079-3082, pl. 1.

Fitzinger, L. I., 1826. *Neue Classification der Reptilien*. Wien, Heubner: i-viii + 1-66, 1 tab.

--- 1843. *Systema Reptilium*. Fasc. 1. *Amblyglossae*. Vindobonae, Braumuller & Seidel: 1-106 + i-ix

Fraser, D. J. & Bernatchez, L. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Molecular Ecology*, **10**: 2741-2752

Freytag, G. E., 1955. Ein neuer Teichmolch aus der Turkei. *Zoologischer Anzeiger*, **154** (9-10): 195-200

--- 1983. Zur systematischen Stellung von *Triturodes caudopunctatus* Liu & Hu, 1973. Morphometrische und röntgenanatomische Befunde (Amphibia, Caudata, Salamandridae). *Zoologische Abhandlungen Staatliches Museum für Tierkunde in Dresden*, **39** (2): 39-49

Frost, D. R. (ed.), 1985. *Amphibian species of the world*. Lawrence, Allen Press & Assoc. Syst. Coll.: [i-iv] + i-v + 1-732.

rost, D. R., Grant, T., Faivovich, J., Bazin, R. H., Haas, A., Haddad, C. F. B., de Sa, R. O., Channing, A., Wilkinson, M., Donnellan, S. C., Raxworthy, C. J., Campbell, J. A., Blotto, B. L., Moler, P., Drewes, R. C., Nussbaum, R. A., Lynch, J. D., Green, D. M. & Wheeler, W. C., 2006. - The amphibian tree of life. *Bulletin of the American Museum of natural History*, **297**: 1-370

uhn, I. E., 1951. Contributiuni la sistematica salamizdrelor din Rep. Pop. Romine. I. Studiul citorva populatii de *Triturus vulgaris* L. *Buletinul de Stiinte Acad. R.P.R., Sect. Biol. Agron. Geol. Geogr.*, Bucuresti, **3** (3): 501-512. [Not seen]

uhn, J. E. & Freytag, G. E., 1952. Über einige Besonderheiten des Teichmolches *Triturus vulgaris vulgaris* in Rumanien und in der Türkei. *Mitt. Naturkd. Vorgesch. Mus. Magdeburg*, **3** (13): 89-96, 3 pl. [Not seen]

Gaffney, E. S., 1977. The side-necked turtle family Chelidae: a theory of relationships using shared derived characters. *American Museum Novitates*, **2620**: 1-28

--- 1979. An introduction to the logic of phylogeny reconstruction. *In*: J. Cracraft & N. Eldredge (ed.), *Phylogenetic analysis and paleontology*, Columbia University Press, New York: 79-111

García-Paris, M., Alcobendas, M., Buckley, D. and Wake, D. B., 2003. - Dispersal of viviparity across contact zones in Iberian populations of fire salamanders (*Salamandra*) inferred from discordance of genetic and morphological traits. *Evolution*, **57** (1). 129-143

García-Paris, M., Montori, A. & Alonso-Zarazaga, M. A., 2004. Apéndice I. Nomenclatura lista de sinónimos y combinaciones. *In*: M. García-París, A. Montori & P. Herrero (ed.), *Fauna Iberica*, **24**, *Amphibia, Lissamphibia*, Madrid, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas: 589-602.

Gené, J., 1839. – Synopsis Reptilium Sardiniae indigenorum. *Memorie della reale Accademia delle Scienze di Torino*, (2), **1**: 257-286, pl. 1-5.

Génermont, J. & Lamotte, M., 1980. Le concept biologique de l'espece dans la zoologie contemporaine. *Mémoires de la Société zoologique de France*, **40**: 427-452.

Gistel, J., 1848. *Naturgeschichte des Thierreichs für hohere Schulen*. Stuttgart, Hoffmann: i-xi + 1-216 + i-iv, pl. 1-32.

Goldfuss, G. A., 1820. *Handbuch der Zoologie*. Dritter Theil, zweite Abtheilung. Nürnberg, Johann Leonhard Schrag: i-xxiv + 1-512, pl. 3-4.

Gorham, S. W., 1974. – *Checklist of world Amphibians up to January 1, 1970. Liste des Amphibiens du monde d'après l'état du 1^{er} janvier 1970*. Saint John, New Brunswick Museum, Lingley Printing Co. Ltd.: 1-173.

Gravenhorst, J. L. C., 1829. – *Deliciae Musei Zoologici Vratislaviensis. Fasciculus primus, continens Chelonios et Batrachia*. Lipsiae, Sumptibus Leopoldi Vossii: i-xiv + 1-106, pl. 1-17.

Gray, J. E., 1850. *Catalogue of the specimens of Amphibia in the collection of the British Museum*. Part II. *Batrachia Gradientia, etc.* London, Spottiswoodes & Shaw: 1-72, pl. 3-4.

----- 1858. Proposal to separate the family of Salamandridae, Gray, into two families, according to the form of the skull. *Proceedings of the zoological Society of London*, **26**: 136-144.

Gronovius, L. T., 1763. – *Zoophylacii Gronoviani*. Fasciculus primus. Lugduni Batavorum, Sumptibus Auctoris: [i-iii] + i-iv + 1-236 + [i], pl. 1-17.

Hamburger, V., 1935. Malformations of hind limbs in species hybrids of *Triton taeniatus* ♀ (and *palmatus* ♀) × *Triton cristatus* ♂. *Journal of experimental Zoology*, **70**: 43-54.

Harlan, R., 1825. Observations on the genus *Salamandra*, with the anatomy of the *Salamandra gigantea* (Barton) or *S. alleghaniensis* (Michaux) and two new genera proposed. *Annals of the Lyceum of natural History of New York*, **1** (2): 222-234, pl. 16-18.

Hayashi, T. & Matsui, M., 1989. Preliminary study of phylogeny in the family Salamandridae: allozyme data. *In*: M. Matsui, T. Hikida & R. C. Goris (ed.), *Current herpetology in East Asia*, Kyoto, Herpetological Society of Japan: 157-167.

Hennig, W., 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin, Deutscher Zentralverlag: [i-vii] + 1-370.

Highton, R., 2000. Detecting cryptic species using allozyme data. *In*: R. C. Bruce, R. C. Jaeger & L. D. Houck (ed.), *The biology of plethodontid salamanders*, New York, Kluwer Academic-Plenum Publishers: 215-241.

Hillis, D. M., Chamberlain, D. A., Wilcox, T. P. & Chippindale, P. T., 2001. – A new species of subterranean blind salamander (Plethodontidae: Hemidactyliini: *Eurycea: Typhlomolge*) from Austin, Texas, and a systematic revision of central Texas paedomorphic salamanders. *Herpetologica*, **57**: 266-280.

Hillis, D. M. & Wilcox, T. P., 2005. Phylogeny of the New World true frogs (*Rana*). *Molecular Phylogenetics & Evolution*, **34**: 299-314.

Hou, M., Zhou, Z.-C., Li, P.-P. & Lu, S.-Q., 2009. Rediscovery of *Pingia granulosus* (Chang, 1933) and description of the neotype specimens [sic]. *Sichuan Journal of Zoology*, **28** (1): 15-18, 3 pl. [In Chinese]

Hu, S.-C., Djao, E.-M. & Liu, C.-C., 1973. A survey of Amphibians and Reptiles in Kweichow Province, including a herpetofaunal analysis. *Acta zoologica sinica*, **19** (2): 149-181. [In Chinese]

Hutchins, M., Duellman, W. E. & Schlager, N., (ed.), 2003. – *Amphibians*. *In*: M. Hutchins (ed.), *Grzimek's animal life encyclopedia*, Second Edition, **6**, Farmington Hills, Michigan, Gale Group: i-xvi + 1-507.

Huxley, J. S., 1957. The three types of evolutionary process. *Nature*, **180**: 454-455.

Iftime, A. & Iftime, O., 2008. Morphological features and possible affinities of some *Lissotriton vulgaris* populations in Nera river area (southwestern Romania). *Russian Journal of Herpetology*, **15** (2): 93-96. [Not seen]

Inger, R. F., 1954. – Systematics and zoogeography of Philippine amphibia. *Fieldiana: Zool.*, **33**: 181-531.

----- 1958. – Comments on the definition of genera *Evolution*, **12** 370-384

----- 1966. – The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana: Zool*, **52**: 1-402.

----- 1996 Commentary on a proposed classification of the family Ranidae. *Herpetologica*, **52** (2). 241-246

Köhler, J., Vieites, D. R., Bonett, R. M., García, F. H., Glaw, F., Steinke, D. & Vences, M., 2005 – New amphibians and global conservation a boost in species discoveries in a highly endangered vertebrate group. *BioScience*, **55** (8): 693-696.

Kolombatović, G., 1907 Contribuzione alla fauna dei vertebrate della Dalmazia. *Glasnika Hrvastkoga Naravoslovnaga Drutva*, Zagreb, **19**: 1-24 [Not seen].

Krizmanić, I., Mesaros, G., Dzukić, G. & Kalezić, M. L., 1997 Morphology of the smooth newt (*Triturus vulgaris*) in former Yugoslavia taxonomical implications and distribution patterns. *Acta zoologica Academiae Scientiarum hungaricae*, **43** (4): 345–357 [Not seen]

Kuntner, M. & Agnarsson, I., 2006 – Are the Linnean and phylogenetic nomenclatural systems combinable? Recommendations for biological nomenclature. *Systematic Biology*, **55**, 774-784

Lantz, L. A., 1934. Molchbastarde. *Blatter fur Aquarien- und Terrarienkunde*, **45** (2) 23-32

---- 1947. Hybrids between *Triturus cristatus* Laur and *Triturus marmoratus* Latr *Proceedings of the zoological Society of London*, **117**: 247-258, pl 1-3

Lanza, B., 1977 – Sympatry and coexistence in the Italian *Triturus*, with notes on the *Molge italica molisana* problem (Amphibia Salamandridae) *Monitore zoologico italiano*, (n s.), **11** 113-118

Larson, A., 1991. A molecular perspective on the evolutionary relationships of the salamander families. *Evolutionary Biology*, **25**. 211-217.

Larson, A., Weisrock, D. W. & Kozak, K. H., 2003 Phylogenetic systematics of salamanders (Amphibia Urodela), a review *In* D. M. Sever (ed.), *Reproductive biology and phylogeny of Urodela*, Enfield (USA) & Plymouth (UK), Science Publishers: 31-108

Latreille, P. A., 1800. *Histoire naturelle des salamandres de France, précédée d'un tableau methodique des autres reptiles.* Paris, Villier: i-xlvii + 1-63, pl. 1-6

---- 1825. *Familles naturelles du règne animal*. Paris, Bailliere: [i-v] + 1-570

Laurenti, J. N., 1768 *Specimen medicum, exhibens synopsin Reptilium emendatam cum experimentis circa venena et antidota Reptilium austriacorum* Viennae, Joan Thom Nob. de Trattnern: i-ii + 1-215, pl 1-5

Leach, W. E., 1818 Cymothoadees, Cymothoadae (Crust.) In *Dictionnaire des sciences naturelles*, **12** (Crit-Daz), Strasbourg & Paris, Levrault & Le Normant: 338-354.

escure, J., 2008 Note explicative à la liste taxinomique actualisee des Amphibiens et Reptiles de France. *Bulletin de la Société herpétologique de France*, **126** 25-36

euckart, S., 1821 – Einiges über die fischartigen Amphibien *Isis von Oken, Litterarischer Anzeiger*, **1821** 257-265, pl 5

innaeus, C., 1758 *Systema Naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* Editio decima, reformata. Tomus I. Holmiae, Laurentii Salvii, [i-iv] + 1-824.

itvinchuk, S. N., Zuiderwijk, A., Borkin, L. J. & Rosanov, J. M., 2005 Taxonomic status of *Triturus vittatus* (Amphibia: Salamandridae) in western Turkey trunk vertebrae counts, genome size and allozyme data *Amphibia-Reptilia*, **26** (3) 305-323

otsy, J. P., 1918 – La quintessence de la théorie du croisement *Archives neerlandaises des Sciences exactes et naturelles*, (III B), **3**. 351-353. [Not seen]

Macgregor, H. C., Sessions, S. K. & Arntzen, J. W., 1990. – An integrative analysis of phylogenetic relationships among newts of the genus *Triturus* (family Salamandridae), using comparative biochemistry, cytogenetics and reproductive interactions. *Journal of evolutionary Biology*, **3** 329-373

Mancino, G., Ragghianti, M. & Bucci-Innocenti, S., 1976 – Chromosome constitution of newt intergeneric hybrids of the genus *Triturus* (Urodela: Salamandridae). *Atti della Accademia nazionale dei Lincei*, **61**: 661-668, pl. 1-7

- 1977. – Cytotaxonomy and cytogenetics in European newt species. *In*: D. H. Taylor & S. I. Guttman (ed.), *The reproductive biology of amphibians*, New York, Plenum Press. 411-477

----- 1978. Experimental hybridization within the genus *Triturus* (Urodela, Salamandridae). I. Spermatogenesis of F_1 species hybrids, *Triturus cristatus carnifex* ♀ × *T. vulgaris meridionalis* ♂. *Chromosoma*, **69**: 27-46.

----- 1979. Experimental hybridization within the genus *Triturus* (Urodela, Salamandridae). II. The lampbrush chromosomes of F_1 species hybrids between *Triturus cristatus carnifex* and *T. vulgaris meridionalis*. *Caryologia*, **32** (1): 61-79.

MARTENS, E. VON, 1885. – Über Vorkommen und Zeichnungs-Varietäten von *Salamandra maculosa*. *Sitzungs-Berichte der Gesellschaft naturforschender Freunde zu Berlin*, **1884** (10): 193-195.

MARTÍNEZ-SOLANO, I., ALCOBENDAS, M., BUCKLEY, D. & GARCÍA-PARÍS, M., 2005. – Molecular characterization of the endangered *Salamandra salamandra almanzoris* (Caudata, Salamandridae). *Annales Zoologici Fennici*, **42**: 57-68.

MARTÍNEZ-SOLANO, I., TEIXEIRA, J., BUCKLEY, D. & GARCÍA-PARÍS, M., 2006. – Mitochondrial DNA phylogeography of *Lissotriton boscai* (Caudata, Salamandridae): evidence for old, multiple refugia in an Iberian endemic. *Molecular Ecology*, **15**: 3375-3388.

MASSALONGO, A., 1853. – Sopra un nuovo genere di Rettili della provincia padovana. *Nuovi Annali delle Scienze naturali*, Bologna, (3), **7**: 5-16, 1 pl.

MAYR, E., 1942. – *Systematics and the origin of species from the viewpoint of a zoologist*. Columbia University Press, New York: i-xiv + 1-334.

----- 1963. – *Animal species and evolution*. Harvard University Press, Cambridge, Mass.: i-xiv + 1-797.

----- 1969. – *Principles of systematic zoology*. New York, McGraw-Hill: i-xiii + 1-428.

----- 1975. – The unity of the genotype. *Biologisches Zentralblatt*, **94**: 377-388.

MAYR, E. & ASHLOCK, 1991. – *Principles of systematic zoology*. Second edition. New York, McGraw-Hill: i-xx + 1-475.

MCCRANIE, J. R., VIEITES, D. R. & WAKE, D. B., 2008. – Description of a new divergent lineage and three species of Honduran salamanders of the genus *Oedipina* (Caudata, Plethodontidae). *Zootaxa*, **1930**: 1-17.

MECHAM, J. S., 1967*a*. – *Notophthalmus perstriatus* (Bishop). Striped newt. *Catalogue of American Amphibians and Reptiles*, **38**: 38.1-38.2.

----- 1967*b*. – *Notophthalmus viridescens* (Rafinesque). Newt. *Catalogue of American Amphibians and Reptiles*, **53**: 53.1-53.4.

----- 1968. – *Notophthalmus meridionalis* (Cope). Southern newt. *Catalogue of American Amphibians and Reptiles*, **74**: 74.1-74.2.

MEEGASKUMBURA, M., BOSSUYT, F., PETHIYAGODA, R., MANAMENDRA-ARACHCHI, K., BAHIR, M., MILINKOVITCH, M. C. & SCHNEIDER, C. J., 2002. – Sri Lanka: an amphibian hot spot. *Science*, **298**: 379.

MERREM, B., 1820. – *Versuch eines Systems der Amphibien. Tentamen systematis amphibiorum*. Marburg, Iohann Christian Krieger: (i-xv + 1-191) I 2, 1 pl.

MERTENS, R. & WERMUTH, H., 1960*a*. – Application to suppress under the plenary powers eleven specific names of Amphibia and Reptilia and to validate thirteen names with their original author and date. Z.N.(S.) 1449. *Bulletin of zoological Nomenclature*, **18**: 3-7.

----- 1960*b*. – *Die Amphibien und Reptilien Europas. (Dritte Liste, nach dem Stand vom 1. Januar 1960)*. Frankfurt am Main, Waldemar Kramer: i-xi + 1-264.

MICHAHELLES, M., 1830. – Neue sudeuropäische Amphibien. *Isis von Oken*, **1830** (2): 189-195, pl. 2.

MICHALAK, P., GRZESIK, J. & RAFINSKI, J., 1998. – Tests for sexual incompatibility between two newt species, *Triturus vulgaris* and *Triturus montandoni*: no-choice mating design. *Evolution*, "1997", **51** (6): 2045-2050.

MICHALAK, P. & RAFIŃSKI, J., 1999. – Sexual isolation between two newt species, *Triturus vulgaris* and *Triturus montandoni* (Amphibia, Urodela, Salamandridae). *Biological Journal of the Linnean Society*, **67** (3): 343-352.

MIKULÍČEK, P. & PIALEK, J., 2003. – Molecular identification of three crested newt species (*Triturus cristatus* superspecies), by RAPD markers. *Amphibia-Reptilia*, **24** (2): 201-207.

MONTORI, A. & HERRERO, P., 2004. – Orden Caudata Scopoli, 1777. *In*: M. GARCÍA-PARÍS, A. MONTORI & P. HERRERO (ed.), *Fauna Iberica*, **24**, *Amphibia, Lissamphibia*, Madrid, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas: 43-275.

MONTORI, A. & LLORENTE, G. A. (ed.), 2005. – *Lista patrón actualizada de la herpetofauna española. Conclusiones de nomenclatura y taxonomía para las especies de anfibios y reptiles de España*. Madrid, Asociacion Herpetologica Española: 1-46.

Montori, A., Llorente, G. A. & García-París, M., 2008. – Allozyme differentiation among populations of the Pyrenean newt *Calotriton asper* (Amphibia, Caudata) does not mirror their morphological diversification. *Zootaxa*, **1945**: 39-50.

Morescalchi, A., 1975. – Chromosome evolution in the Caudate Amphibia. *Evolutionary Biology*, **8**: 339-387.

Moritz, C., 1994. – Defining "Evolutionary Significant Units" for conservation. *Trends in Ecology & Evolution*, **9**: 373-375.

Nascetti, G., Andreone, F., Capula, M. & Bullini, L., 1988. – A new *Salamandra* species from southwestern Alps (Amphibia, Urodela, Salamandridae). *Bolletino del Museo regionale di Scienze naturali*, Torino, **6** (2): 617-638. [Not seen].

Nesterov, P. V., 1916. – Trois formes nouvelles d'amphibies (Urodela) du Kurdistan. *Informations sur l'Activité du Musée zoologique de l'Académie des Sciences*, Saint-Petersbourg, **21**: 1-30, pl. 1-3.

Ng, P. K. L., 1994. – The citation of species names and the role of the author's name. *Raffles Bulletin of Zoology*, **42** (3): 509-513.

Nikolsky, A. M., 1918. – Amphibiens (Amphibia). *In*: N. V. Nasonov (ed.), *Faune de la Russie et des pays limitrophes*, Petrograd: 1-311, 4 tab. [In Russian].

Nussbaum, R. A. & Brodie, E. D., 1981*a*. – *Taricha* (Gray). Pacific newts. *Catalogue of American Amphibians and Reptiles*, **271**: 271.1-271.2.

---- 1981*b*. – *Taricha granulosa* (Skilton). Rough-skinned newt. *Catalogue of American Amphibians and Reptiles*, **272**: 272.1-271.4.

---- 1981*c*. – *Taricha torosa* (Rathke). California newt. *Catalogue of American Amphibians and Reptiles*, **273**: 273.1-273.4.

Olgun, K., Baran, I. & Tok, C. V., 1999. – The taxonomic status of *Triturus vulgaris* (Linnaeus, 1758) populations in western Anatolia, Turkey. *Turkish Journal of Zoology*, **23**: 133-140.

Padial, J. M. & de la Riva, I., 2007. – Taxonomy, the Cinderella of science, hidden by its evolutionary stepsister. *Zootaxa*, **1577**: 1-2.

Pariser, K., 1932. – Verschiebung des Geschlechtsverhaltnisses bei künstlich erzeugten Tritonbastarden. *Biologisches Zentralblatt*, **52** (11-12): 654-659.

---- 1935. – Deformidades y otras anomalias en hibridos interespecíficos del genero *Triton* (Anfibios). *Revista española de Biologia*, **4** (1): 5-12.

---- 1936. – El derarrollo y la relación numerica entre los sexos en los hibridos interespecificos obtenidos por fecundación artificial en el genero *Triton* (*Molge*). *Revista española de Biologia*, **5**: 11-93, pl.

Parra, G., Brown, R., Hanken, J., Hedges, B., Heyer, R., Kuzmin, S., Lavilla, E., Lötters, S., Pimenta, B., Richards, S., Rödel, M. O., de Sá, R. O. & Wake, D., 2005. – Systematics and conservation. *In*: C. Gascon, J. P. Collins, R. D. Moore, D. R. Church, J. E. McKay & J. R. Mendelson III (ed.), *Amphibian Conservation Action Plan*, Gland (Switzerland) & Cambridge (UK), IUCN/SSC Amphibian Specialist Group: 45-48.

Parra-Olea, G., García-París, M. & Wake, D. B., 2004. – Molecular diversification of salamanders of the tropical American genus *Bolitoglossa* (Caudata, Plethodontidae) and its evolutionary and biogeographical implications. *Biological Journal of the Linnean Society*, **81**: 325-346.

Pecio, A. & Rafinski, J., 1985. – Sexual behaviour of the Montandon's newt, *Triturus montandoni* (Boulenger) (Caudata: Salamandridae). *Amphibia-Reptilia*, **6**: 11-22.

Peracca, M. G., 1886. – Sulla bontà specifica del *Triton Blasii* de l'Isle e descrizione di una nuova forma ibrida di Tritone francese. *Bollettino dei Musei di Zoologia ed Anatomia comparata della reale Università di Torino*, **1** (12): 1-13, 1 pl.

---- 1898. – Descrizione di una nuova specie di tritone italiano. *Bollettino dei Musei di Zoologia ed Anatomia comparata della reale Università di Torino*, **13** (317): 1-6.

Poll, H., 1909. – Mischlinge von *Triton cristatus* Laur. und *Triton vulgaris* L. *Biologisches Zentralblatt*, **29**: 30-31.

Radovanović, M., 1951. – A new race of the Alpine newt from Yugoslavia. *British Journal of Herpetology*, **1** (5): 93-97.

Raffaëlli, J., 2007. – *Les Urodeles du monde*. Plumelec, Penclen edition: [i-vi] + 1-377.

Rafinesque, C. S., 1815. – *Analyse de la nature ou Tableau de l'univers et des corps organisés*. Palerme, Jean Barravecchia: 1-124, 1 pl.

----- 1819. Prodrome de 70 nouveaux genres d'animaux découverts dans l'intérieur des Etats-Unis d'Amérique, durant l'annee 1818 *Journal de Physique, de Chimie et d'Histoire naturelle*, **88** 417-429

----- 1820. - *Annals of nature, or annual synopsis of new genera and species of animals, plants, &c discovered in North America First annual number, for 1820* Lexington, Thomas Smith 1-16.

----- 1836 *A life of travels and researches in North America and South Europe, or, outlines of the life, travels and researches of C. S. Rafinesque* Philadelphia, Turner, 1-148

Rafiński, J, Cogalniceanu, D & Babik, W, 2001 Genetic differenciation of the two subspecies of the smooth newt *Triturus vulgaris vulgaris* and *Triturus vulgaris ampelensis* inhabiting Romania as revealed by enzyme electrophoresis. *Folia Biologica*, Krakow, **49**· 239-245.

Ragghianti, M, Bucci Innocenti, S & Mancino, G, 1980 Chromosome polymorphism in the Italian newt, *Triturus italicus*. *Chromosoma*, **77**. 333-345.

Ragghianti, M & Wake, D, 1986 - Genic variation and its evolutionary implications in the Italian newt, *Triturus italicus*. *Herpetologica*, **42** (2): 206-214

Rathke, M H, 1833 Fünftes Heft *In* F Eschscholtz, *Zoologischer Atlas, enthaltend Abbildungen und Beschreibungen neuer Thierarten*, Berlin, G. Reimer: i-viii + 1-28, pl 21-25.

Raxworthy, C J., 1988 A description and study of a new dwarf sub-species of smooth newt, *Triturus vulgaris*, from western Anatolia, Turkey *Journal of Zoology*, London, **215**. 753-763.

----- 1990 - A review of the smooth newt (*Triturus vulgaris*) subspecies, including an identification key *Herpetological Journal*, **1** (11): 481-492.

Razoumowsky, Comte G. de, 1789. *Histoire naturelle du Jorat et de ses environs* Tome premier Lausanne, Jean Mourer: i-xvi + 1-322, pl. 1-3

Riberon, A, Miaud, C, Guyetant, R & Taberlet, P., 2004 Genetic variation in an endemic salamander, *Salamandra atra*, using amplified fragment polymorphism. *Molecular Phylogenetics & Evolution*, **31**· 910-914

Riley, N D & China, W E, 1962 Opinion 642 Suppression under the plenary powers of eleven specific names of Reptilia and Amphibia with validation of thirteen specific names with their original authors and dates. *Bulletin of zoological Nomenclature*, **19** (5)· 280-283

Ryder, O. A, 1986 - Species conservation and systematics the dilemma of subspecies. *Trends in Ecology & Evolution*, **1**, 9-10

Salthe, S. N, 1967 Courtship patterns and the phylogeny of the Urodeles. *Copeia*, **1967** 100-117.

Samadi, S. & Barberousse, A, 2006 - The tree, the network, and the species. *Biological Journal of the Linnean Society*, **89**: 509-521.

Sarasin P & Sarasin, F, 1890 Zur Entwicklungsgeschichte und Anatomie der ceylonesischen Blindwuhle *Ichthyophis glutinosus*, L Vierter Theil *In Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon*, Zweiter Band, Wiesbaden, Kreidel: 151-263, pl. 15-24

Sauvage, H. E, 1876 Sur quelques Batraciens de la Chine. *L'Institut, Journal universel des Sciences et des Sociétés savantes*, (n.s.), **4** (189)· 274-275.

Savi, P, 1821 Descrizione (inedita) di una nuova specie di Salamandra terrestre, *Salamandra perspicillata* Nob. *Biblioteca italiana ossia Giornale di Letteratura Scienze ed Arti*, Milano, **22** (2) 228-230

--- 1838 Descrizione della *Salamandra corsica*, e della *Megapterna montana*, nuovi animali della famiglia dei Batrachii. *Nuovo Giornale dei Letterati*, Pisa, **37** 208-217

Schlosser, J A, 1768 *Over de Amboinsche Haagdis* De Lacerta amboinensi Amsterdam, Schlosser [i-iii] + 1-18 I 2 + [i], 1 pl.

Schmidt, K P, 1927. Notes on Chinese amphibians. *Bulletin of the American Museum of natural History*, **54**. 553-575, pl. 31-32

Schmidtler, J F., 2004. Der Teichmolch (*Triturus vulgaris* (L.)), ein Musterbeispiel für systematische Verwechslungen und eine Flut von Namen in der fruhen Erforscgungsgeschichte *Sekretär*, **4** (2) 10-28

Schneider, I G, 1799 *Historiae Amphibiorum naturalis et literariae Fasciculus primus, continens Ranas, Calamitas, Bufones, Salamandras et Hydros in genera et species descriptos notisque suis distinctos*. Jena, Frommann. i-xv + 1-264, pl 1-2

Schreitmuller W, 1910 Gegluckte Bastardierungen verschiedener Molcharten *Blatter fur Aquarien und Terrarienkunde*, **21**. 215-217

Seliškar, A. & Pehani, H., 1935. Limnologische Beitrage zum Problem der Amphibienneotenie (Beobachtungen an Tritonen der Triglavseen). *Verhandlungen der internationalen Vereinigung fur theoretische und angewandte Limnologie*, Beograd, **7** (1): 263-294.

Simpson, G. G., 1940. Types in modern taxonomy. *American Journal of Science*, **238**: 413-431.

Smith, H. M. & Perez-Higareda, G., 1986. Nomenclatural name-forms. *Systematic Zoology*, **35**: 421-422.

Sonnini, C. S. & Latreille, P. A., 1801*a*. *Histoire naturelle des reptiles*. Tome **1**. Premiere partie. *Quadrupèdes et bipèdes ovipares*. Paris, Deterville: [i-iii] + i-xxii + 1-332, 14 pl.

---- 1801*b*. *Histoire naturelle des Reptiles*. Tome **4**. Seconde partie. *Serpens*. Paris, Deterville: [i-iii] + 1-410, 14 pl.

Sotiropoulos, K., Eleftherakos, K., Džukić, G., Kalezić, M. L., Legakis, A. & Polymeni, R. M., 2007. Phylogeny and biogeography of the Alpine newt *Mesotriton alpestris* (Salamandridae, Caudata), inferred from mtDNA sequences. *Molecular Phylogenetics & Evolution*, **45**: 211-226.

Sotiropoulos, K., Eleftherakos, K., Kalezić, M. L., Legakis, A. and Polymeni, R. M., 2008. – Genetic structure of the Alpine newt, *Mesotriton alpestris* (Salamandridae, Caudata), in the southern limit of its distribution: implications for conservation. *Biochemical Systematics & Ecology*, **36** (4), 297-311.

Sparreboom, M., Steinfartz, S. & Schultschik, G., 2000. Courtship behaviour of *Neurergus* (Caudata: Salamandridae). *Amphibia-Reptilia*, **21**: 1-11.

Speybroeck, J. & Crochet, P. A., 2007. Species list of the European herpetofauna: a tentative update. *Podarcis*, **8** (1-2): 8-34.

Steindachner, F., 1888. Über eine neur *Molge* Art und eine Varietat von *Homalopsis Doriae* Pet. *Sitzungsberichte der mathematische-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften*, Wien, "1887", **96** (2): 69-72, pl. 1.

Steinfartz, S., Hwang, U. W., Tautz, D., Öz, M. & Veith, M., 2002. Molecular phylogeny of the salamandrid genus *Neurergus*: evidence for an intrageneric switch of reproductive biology. *Amphibia-Reptilia*, **23**: 419-431.

Steinfartz, S., Veith, M. & Tautz, D., 2000. Mitochondrial sequence analysis of *Salamandra* taxa suggests old splits of majot lineages and postglacial recolonizations of central Europe from distinct source populations of *Salamandra salamandra*. *Molecular Ecology*, **9**: 397-410.

Steinfartz, S., Vicario, S., Arntzen, J. W. & Caccone, A., 2007. A Bayesian approach on molecules and behavior: reconsidering phylogenetic and evolutionary patterns of the Salamandridae with emphasis on *Triturus* newts. *Journal of experimental Zoology (Mol. Dev. Evol.)*, **308** (B): 139-162.

Stejneger, L., 1936. Types of amphibian and reptilian genera proposed by Laurenti in 1768. *Copeia*, **1936**: 133-141.

Strauch, A., 1870. Revision der Salamandriden-Gattungen nebst Beschreibung einiger neuen oder weniger bekannten Arten dieser Familie. *Mémoires de l'Académie impériale des Sciences de Saint Petersburg*, (7), **16** (4): [i-ii] + 1-110, pl. 1-2.

Stuart, B. L. & Papenfuss, T. J., 2002. A new salamander of the genus *Paramesotriton* (Caudata: Salamandridae) from Laos. *Journal of Herpetology*, **36**: 145-148, 1 pl.

Stuart, S., Hoffmann, M., Chanson, D., Cox, N., Berridge, R., Ramani, P. & Young, B., 2008. Threatened amphibians of the world. Barcelona (Lynx Edition), Gland (IUCN) & Arlington (Conservation Intenational): i-xv + 1-758.

Swainson, W., 1839. *The natural history of Fishes, Amphibians, & Reptiles or Monocardian Animals*. 2. London, Longman & Co.: i-vi + 1-452.

Szalay, F. S., 1977. Phylogenetic relationships and a classification of the eutherian Mammalia. *In*: M. K. Hecht, P. Goody & B. M. Hecht (ed.), *Major patterns in vertebrate evolution*, New York, Plenum Press: 315-374.

Taylor, E. H., 1962. The amphibian fauna of Thailand. *University of Kansas Science Bulletin*, **63**: 265-599.

Temminck, C. J. & Schlegel, H., 1838. Les Batraciens. *In*: P. F. de Siebold & W. de Haan (ed.), *Fauna Japonica*, Lugduni Batavorum, J. G. Lalau: 105-140, pl. 2-8.

Templeton, A. R., 1989. The meaning of species and speciation: a genetic perspective. *In*: D. Otte & J. A. Endler (ed.), *Speciation and its consequences*, Sunderland, Mass., Sinauer: 3-27.

Thireau, M., 1986. *Catalogue des types d'Urodeles du Muséum national d'Histoire naturelle*. Paris, MNHN: 1-96.

Thorn, R., 1969. – *Les salamandres d'Europe, d'Asie et d'Afrique du Nord*. Paris, Lechevalier, "1968": 1-376.

Thorn, R. & Raffaëlli, J., 2001. – *Les salamandres de l'ancien monde*. Paris, Boubée: 1-449.

Titus, T. A. & Larson, A., 1995. – A molecular phylogenetic perspective on the evolutionary radiation of the salamander family Salamandridae. *Systematic Biology*, **44** (2): 125-151.

Tourneville, A., 1879. – Description d'une nouvelle espece de Batracien Urodele d'Espagne (*Pelonectes Boscai* Lataste). *Bulletin de la Société zoologique de France*, **4**: 69-88, pl. 7.

Tschudi, J. J., 1838. – *Classification der Batrachier, mit Berucksichtigung der fossilen Thiere dieser Abtheilung der Reptilien*. Neuchâtel, Petitpierre: i-ii + 1-98, pl. 1-6.

Turesson, G., 1929. – Zur Natur und Begrenzung der Arteinheiten. *Hereditas*, **12**: 323-334.

Twitty, V. C., 1935. – Two new species of *Triturus* from California. *Copeia*, **1935** (2): 73-80.

----- 1964. – *Taricha rivularis* (Twitty). Red-bellied newt. *Catalogue of American Amphibians and Reptiles*, **9**: 9.1-9.2.

----- 1966. – *Of scientists and salamanders*. San Francisco, Freeman: 1-178.

Unterstein, W., 1930. – 2. Schwanzlurche. *In*: R. Mell, W. Unterstein, E. Ahl & H. Hanberg [sic, for Kanberg], Beitrage zur Lurch- und Kriechtierfauna Kwangsi's. *Sitzungsberichte der Gesellschaft Naturforschender Freund zu Berlin*, **1930**: 313-315.

Van der Hoeven, J., 1833. – *Handboek der Dierkunde, of grondbeginsels der natuurlijke geschiedenis van het dierenrijk*. Tweeden deels. Amsterdam, Sulpke: [i-v] + i-ii + i-x + i-v + 1-698.

Van Valen, L., 1973. – Are categories in different phyla comparable? *Taxon*, **22**: 333-373.

Veith, M., Mayer, C., Samraoui, B., Barroso, D. D. & Bogaerts, S., 2004. – From Europe to Africa and vice versa: evidence for multiple intercontinental dispersal in ribbed salamanders (genus *Pleurodeles*). *Journal of Biogeography*, **31**: 159-171.

Veith, M., Steinfartz, S., Zardoya, R., Seitz, A. L. & Meyer, A., 1998. – A molecular phylogeny of "true" salamanders (family Salamandridae) and the evolution of terrestriality of reproductive modes. *Journal of zoological Systematics & evolutionary Research*, **36** (1-2): 7-16.

Venczel, M., 2008. – A new salamandrid amphibian from the Middle Miocene of Hungary and its phylogenetic relationships. *Journal of Systematic Paleontology*, **6** (1): 41-59.

Verity, R., 1925. – Remarks on the evolution of the Zygaenae and an attempt to analyse and classify the variations of *Z. lonicerae*, Scheven, and of *Z. trifolii*, Esp., and other subspecies. *The Entomologist's Record & Journal of Variation*, **37** (7-8): 101-104.

Vieites, D. R., Min, M. S. & Wake, D. B., 2007. – Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. *Proceedings of the national Academy of Sciences of the USA*, **104** (50): 19903-19907.

Wagler, J., 1830. – *Naturliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vogel*. Munchen, Stuttgart & Tubingen, Cotta: i-vi + 1-354.

Wake, D. B. & Özeti, N., 1969. – Evolutionary relationships in the family Salamandridae. *Copeia*, **1969** (1): 124-137.

Warren, L., 2004. – *Constantine Samuel Rafinesque: a voice in the American wilderness*. Lexington, University Press of Kentucky: 1-252.

Weisrock, D. W., Harmon, L. J. & Larson, A., 2005. – Resolving the deep phylogenetic relationships among salamander families: analyses of mitochondrial and nuclear genomic data. *Systematic Biology*, **54** (5): 758-777.

Weisrock, D. W., Macey, J. R., Ugurtas, I. H., Larson, A. & Papenfuss, T. J., 2001. – Molecular phylogenetics and historical biogeography among salamandrids of the "true" salamander clade: rapid branching of numerous highly divergent lineages in *Mertensiella luschani* associated with the rise of Anatolia. *Molecular Phylogenetics & Evolution*, **18** (3): 434-448.

Weisrock, D. W., Papenfuss, T. J., Macey, J. R., Litvinchuk, S. N., Polymeni, R., Ugurtas, I. H., Zhao, E., Jowkar, H. & Larson, A., 2006. – A molecular assessment of phylogenetic relationships and lineage accumulation rates within the family Salamandridae (Amphibia, Caudata). *Molecular Phylogenetics & Evolution*, **41**: 368-383.

Werner, F., 1902. – Eine neue Varietat des Alpenmolches aus Bosnien: *Molge alpestris* var. *Reiseri*. *Verhandlungen der zoologisch-botanischen Gesellschaft in Wien*, **52**: 7-9.

Wheeler, Q. D., Raven, P. H. & Wilson, E. O., 2004. – Taxonomy: impediment or expedient? *Science*, **303**: 285.

Wolterstorff, W., 1905. – Über *Triton vulgaris* L. subsp. *graeca* Wolt. n. subsp. *Zoologischer Anzeiger*, **29** (5): 137-139.

----- 1908. Zur Kenntnis der Tritonen Südosteuropas. I. Ueber Kreuzungsversuche zwischen *Triton* (= *Molge*) *vulgaris* L. subsp. *typica* Wolt., *meridionalis* Blgr., *graeca* Wolt. *Lacerta*, Beilage zu *Wochenschrift für Aquarien - und Terrarienkunde*, Braunschweig, **4-5**. 1-2.

----- 1909a. Über Polls Bastarde zwischen *Triton cristatus* Laur. u. *Triton vulgaris* L. *Zoologischer Anzeiger*, **33** (26): 850-857.

----- 1909b. Ueber Polls Bastarde zwischen *Triton cristatus* Laur. und *Triton vulgaris* L. *Blatter fur Aquarien- und Terrarienkunde*, **20** (24): 373-379.

----- 1910. Einiges über Molchbastarde. *Abhandlungen und Berichte aus dem Museum für Natur- und Heimatkunde und dem naturwissenschaftlichen Verein in Magdeburg*, **2**: 25-29.

----- 1911. Neues von Polls Bastarden zwischen *Triton cristatus* ♂ und *Triton vulgaris* ♀. *Abhandlungen und Berichte aus dem Museum fur Natur- und Heimatkunde und dem naturwissenschaftlichen Verein in Magdeburg*, **2**. 108-112.

----- 1914. Zwei neue Tritonenformen der paläarktischen Region. *Abhandlungen und Berichte aus dem Museum für Natur- und Heimatkunde und dem naturwissenschaftlichen Verein in Magdeburg*, **2**: 371-381.

----- 1925. Katalog der Amphibien Sammlung im Museum für Natur- und Heimatkunde zu Magdeburg. Erster Teil. Apoda, Caudata. *Abhandlungen und Berichte aus dem Museum für Natur- und Heimatkunde und dem naturwissenschaftlichen Verein in Magdeburg*, **4** (2): 231-310.

----- 1934. - Über die Gattung *Hypselotriton*. *Zoololischer Anzeiger*, **108**: 257-263.

Ye, C., Fei, L. & Hu, S., 1993. – *Rare and economic amphibians of China*. Chengdu, Sichuan Publishing House of Science and Technology: [i-iii] + 1-2 + 1-2 + 1-7 + 412. [In Chinese]

Zhang, P., Papenfuss, T. J., Wake, M. H., Qu, L. & Wake, D. B., 2008. Phylogeny and biogeography of the family Salamandridae (Amphibia. Caudata) inferred from complete mitochondrial genomes. *Molecular Phylogenetics & Evolution*, **49**: 586-597.

Zhao, E.-M. & Adler, K., 1993. *Herpetology of China*. Oxford, Ohio, USA, SSAR: 1-522 + [i-v], pl. 1-48 + 1.

Zhao, E. & Hu, Q., 1984. *Studies on Chinese tailed amphibians*. Chengdu, Sichuan Scientific & Technical Publishing House: [i-v] + 1-68, 3 pl.

----- 1988. The classification and evolution of the Chinese Salamandridae. *In*: Zhao, E., Hu, Q., Jiang, Y. & Yang, Y. (ed.), *Studies on Chinese Salamanders*, *in*: *Contributions in Herpetology*, **4**, SSAR, Oxford (Ohio): 12-26.

Corresponding editor: Annemarie Ohler

Alytes, 2009, **26** (1-4): 86-96.

The tadpole of *Quasipaa fasciculispina* (Inger, 1970) from southeastern Thailand, with the description of its buccal anatomy

Chantip INTHARA[*,**], Yodchaiy CHUAYNKERN[*,***],
Prateep DUENGKAE[****] & Stéphane GROSJEAN[*]

[*] Muséum national d'Histoire naturelle, Departement Systematique et
Evolution, UMR 5202 CNRS OSEB, Reptiles et Amphibiens,
Case 30, 25 rue Cuvier, 75005 Paris, France

[**] Department of Biology, Faculty of Science, Khon Kaen University,
Muang, Khon Kaen 40002, Thailand

[***] Thailand Natural History Museum, National Science Museum,
National Science Museum, Technopolis, Khlong 5,
Khlong Luang, Pathum Thani 12120, Thailand

[****] Department of Forest Biology, Faculty of Forestry, Kasetsart University,
Jatujak, Bangkok 10900, Thailand

We provide a description of the larva of *Quasipaa fasciculispina* (Inger, 1970) from the type locality: Khao Soi Dao Wildlife Sanctuary, Chanthaburi Province, Thailand. The buccal features are also described. This tadpole is compared to the other known tadpoles of the genus *Quasipaa* Dubois, 1992. It differs from them by the following combination of characters: tadpole of large size, the largest after *Q. verrucospinosa* (Bourret, 1937); KRF 2:5+5/1+1:2; three rows of papillae on the lower labium; and numerous black spots on the tail without a transverse bar between tail and body. This tadpole is used for consumption by local people.

INTRODUCTION

Quasipaa fasciculispina was described from southeastern Thailand by INGER (1970) as *Rana fasciculispina*. The generic placement of this species changed several times (DUBOIS, 1987, 1992; JIANG et al., 2005; FROST et al., 2006) and we here follow OHLER & DUBOIS (2006) in considering it as a member of the genus *Quasipaa* Dubois, 1992. This species is currently known from southeastern Thailand (Chanthaburi Province) and southwestern Cambodia (INGER, 1970; KHONSUE & THIRAKHUPT, 2001; BRINGSOE, 2002; LAUHACHINDA et al., 2002; NOIKOTR & LAUHACHINDA, 2002; OHLER et al., 2002; NABHITABHATA et al., 2004; OHLER & DUBOIS, 2006; STUART & EMMETT, 2006; GRISMER et al., 2007). In Thailand, even though this species has been known for more than 38 years by science and for a long time by local people who collected this frog and its tadpoles for consumption, the knowledge on this species is poor. At present, this species has been listed as Vulnerable in the Thai Red List (NABHITABHATA & CHAN-ARD, 2005) and is also listed as a Protected Animal of Thailand by the Thai law.

Tadpoles of *Quasipaa fasciculispina* were reared by the first author and described in her master degree (INTHARA, 2000). Then INTHARA et al. (2005) provided information on distribution, a drawing of the oral disc and a life photo (in lateral view) of the tadpole of *Q. fasciculispina*. Recently, we obtained a few tadpole specimens from the type locality of *Q. fasciculispina*. We describe here their external morphology and their buccopharyngeal anatomy, and give illustrations of the tadpole of this species.

MATERIALS AND METHODS

Two tadpoles were captured in the type locality of *Quasipaa fasciculispina* (Khao Soi Dao Wildlife Sanctuary, Chanthaburi Province, Thailand) by hand at night and preserved in a mixed solution of 10 % formalin and 70 % ethanol with a ratio of 50:50. The specimens were deposited at the Thailand Natural History Museum (THNHM), Pathum Thani, Thailand, and were loaned for study to the Muséum national d'Histoire naturelle (MNHN), Paris, France.

The tadpoles correspond in external morphology, oral disc and keratodont row formula to the specimen shown and described by INTHARA (2000). Our identification matches the identification of local people who recognize this tadpole as belonging to *Quasipaa fasciculispina*. This taxon is also the only species of the tribe Paini (DUBOIS, 1992; OHLER & DUBOIS, 2006) known from southeastern Thailand. For all these reasons, we assigned these tadpoles to *Quasipaa fasciculispina*.

The illustrations of the larva, oral disc and buccal anatomy were made using a Leica MS5 stereomicroscope with the help of a camera lucida. Morphological terminology follows ALTIG & MCDIARMID (1999), whereas keratodont row formula is given according to DUBOIS (1995). Developmental stages follow GOSNER (1960). Measurements were made with a graduated ocular attached to a stereomicroscope except for TL which was measured with a digital caliper to the nearest 0.1 mm. The landmarks are those shown in ALTIG & MCDIARMID (1999: 26, figure 3.1), and the additional ones used by GROSJEAN (2006). The abbreviations used are: A2R, length of the second keratodont row on the upper labium; BH, maximum height of body; BL, body length; BW, maximum width of body; DG, length of the dorsal papilla gap; ED, maximum diameter of eye; KRF, keratodont row formula; LF, maximum height of lower tail fin; MTH, maximum tail height; NN, internarial distance; NP, naripupilar distance; ODW, oral disc width; PP, interpupilar distance; RN, rostro-narial distance; SS, distance from tip of snout to opening of spiracle; SU, distance from tip of snout to insertion of upper tail fin; SVL, snout-vent length; TAL, tail length (distance from opening of vent to tip of tail); TL, total length; TMH, maximum height of tail muscle; TMW, maximum width of tail muscle; UF, maximum height of upper tail fin.

RESULTS

Quasipaa fasciculispina (Inger, 1970)
(fig. 1-2)

Material examined. THNHM 13108.1-2 (field numbers Y 0862.1-2, stages 37 and 28 respectively) from Khao Soi Dao Wildlife Sanctuary, Chanthaburi Province, Thailand. Collected on 7 August 2006 by Y. Chuaynkern. Raw measurements of the two specimens examined are given in table 1.

Larval diagnosis. Large tadpole; body stout, oval, tail fin with black spots but without a transverse bar between tail and body; beak undivided, outer surface of lower beak smooth, upper beak dimpled on the middle; KRF 2.5+5/1+1.2, three rows of papillae on the lower labium.

Larval description. Based on the specimen THNHM 13108.2, stage 28, TL 77.7 mm, BL 23.9 mm. Body in lateral view (fig. 1a) oval (quite obtuse), snout nearly rounded, in dorsal view (fig. 1b) body elliptical, snout semicircular, BW 120 % of BH. Eyes of moderate size, ED 9.7 % of BL, bulging and not visible in ventral view, positioned and directed dorsolaterally. Nares round, of small size, rimmed, positioned and directed anterolaterally, closer to tip of snout than to pupils, RN 64 % of NP, NN 60 % of PP. Spiracle single, sinistral, square, of small size, at mid-distance between snout and anal tube opening; in ventrolateral position, oriented posterodorsally, free from body over most of its length; SS 48 % of BL, opening in a plane which would go through a zone comprised between beginning of caudal myotomes and hind limbs. Tail musculature strong, TMH 71 % of BH and 59 % of MTH, gradually tapering and almost reaching tail tip. Tail fins of moderate size; UF 32 % of MTH, LF 27 % of MTH; upper fin not extending onto body, SU 83 % of BL, slightly convex, lower fin not extending onto body, convex, MTH 121 % of BH, tail tip subelliptical with slight point. Anal tube (fig. 1c) of approximately conical shape, medial and entirely attached to ventral fin, opening on lateral right side, posteriorly directed. Oral disc (fig. 2) positioned and directed anteroventrally, emarginated, of large size, ODW 31 % of BL and 55 % of BW, elliptical with a median notch on the lower labium. A row of papillae at the lateral sides of upper labium, 13 submarginal papillae, 3 papilla rows on lower labium. No denticulate papillae. One large papilla gap on the upper labium, no gap on the lower labium, DG 59 % of ODW. KRF 2:5+5/1+1.2, rows of upper labium subequal, A3 with a short gap, lower rows subequal. Jaw sheaths moderately sized, black in color with fine serrations; upper sheath reverse V-shaped with its median part dimpled, lower sheath V-shaped (quite wide). Pineal ocellus present at the level of anterior edge of eyes. Lateral line present: 1st lateral line beginning at margin of mouth, continuing above nares and eyes then curving ventrally and finishing at margin of snout, 2nd line continuing from eyes along side of body until tail, 3rd line beginning from snout, continuing above spiracle and reaching tail.

Coloration. In preservative. Body creamy with dark pigmentation, ventral side gray, tail creamy white with numerous black spots, getting denser in posterior part of tail, posterior

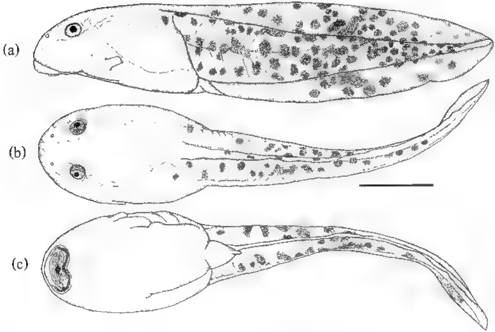
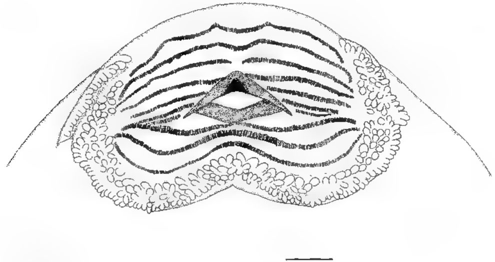


Fig. 1 Drawing of a tadpole of *Quasipaa fasciculispina* (Inger, 1970) (based upon THNHM 13108 2, Gosner's stage 28): (a) lateral, (b) dorsal and (c) ventral views. Scale bar. 10 mm.



ig. 2 Oral disc of *Quasipaa fasciculispina* (Inger, 1970) (based upon THNHM 13108 2, Gosner's stage 28) Scale bar 1 mm

Table 1. Measurements (in millimetres) of tadpoles of *Quasipaa fasciculispina* (Inger, 1970). The tip of the tail of the specimen in stage 37 is damaged, hence a shorter total length and tail length. Abbreviations are given in the *Material and methods* section.

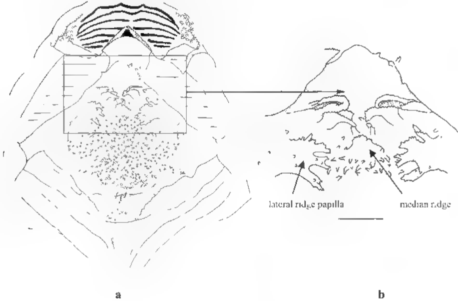
Measurement characters	THMHN 13108.1, stage 37	THMHN 13108.2, stage 28	Measurement characters	THMHN 13108.1, stage 37	THMHN 13108.2, stage 28
TL	71.88	77.67	ED	2.47	2.32
BL	23.97	23.91	TAL	40.60	47.04
SVL	31.28	31.28	UF	4.64	4.35
SS	13.49	11.46	LF	3.77	3.63
SU	21.34	19.79	MTH	14.22	13.49
BH	11.90	11.17	TMH	7.98	7.98
BW	14.22	13.35	TMW	6.96	6.96
PP	7.54	7.11	ODW	7.38	7.38
NN	4.35	4.24	DG	4.35	4.35
RN	2.61	2.32	A2R	4.91	5.28
NP	3.77	3.63	KRF	2.5+5.1+1.1	2.5+5.1+1.1

part of tail dark (see fig. 1). *In life*: Body brown with dark dots, tail creamy brown with numerous black spots.

Buccal description. Based on the specimen THNHM 13108.1, stage 37.

Roof (fig. 3). *Prenarial arena* with high medial ridge, top of ridge smooth, side with 3-5 short papillae. *Choanae* narrow, slightly oblique, internarial distance about 1/5 length of choanae, anterior wall pustular; no papilla on the narial valve. *Postnarial arena* with large postnarial papillae with 4-5 short branches, extremity of each branch curved down, top of postnarial papillae wide, with pustules arranged in 4 rows, 4 short pustulose papillae directed anteromedially lying anterior to median ridge, 1st papilla very short and the other arranged in pairs. Median ridge triangular, much wider than long, jagged. *Lateral ridge papilla* with 4-5 deep branches, each branch with pustules, some branches bifurcate. *Buccal roof arena* oval, wider posteriorly than anteriorly, one long buccal roof arena papilla curved down on each side posterior to lateral ridge, interior of arena with numerous both short and long papillae, highest papilla on each lateral border, most of lateral roof papillae directed medially, posterior part with melanic pigments; 16 short papillae anteriorly to esophageal funnel. *Posterolateral ridge* formed of moderately high and numerous papillae. No glandular zone. *Dorsal velum* discontinue, margin curved, medial portion curving towards esophagus.

Floor (fig. 4). *Prelingual arena* square, its floor smooth except the presence of a low ridge anterior to tongue anlage bearing two pairs of small papillae. Three pairs of infralabial papillae, the most anterior pair short with 6-8 pustules, the second pair long with 10-12 pustules, and the third pair on the posterolateral corner of the arena. Infralabial papillae of the third pair as very large palmate projections of butterfly wing shape (continuous with the anterior infralabial papillae), these palmate projections bearing numerous pustules and short papillae, anterior end of palmate projection attached to posterolateral part of prelingual



ig. 3 Buccal roof of *Quasipaa fasciculispina* (based upon THNHM 13108 2, Gosner's stage 28): (a) general view; (b) anterior part. Scale bar: 1 mm.

arena, posterior end of palmate projection folded down and freely moveable. Both palmate projections having the possibility to get in contact with each other if posterior part expanded, but normally each palmate projection bended down so forming a large gap between them. *Tongue anlage* elliptically shaped (almost round), bearing 4 papillae, a medial and a lateral pair; medial pair long, with 3-6 small pustules on both sides (anteriorly more numerous than posteriorly), lateral pair shorter, with pustules. *Buccal floor arena* about as wide as long, anterior part with only 10 papillae inside the arena, each bearing 2-3 branches, medial and posterior part (corresponding to about 3/4 of buccal floor length) covered with numerous hort and long papillae and some pustules, the posterolateral parts of floor with densely set papillae, anteromedially to buccal pockets with 3 large papillae on each side with pustulose xtremities. Anterior to buccal pockets presence of a bunch of short and long papillae. *Buccal ockets* elliptical, transverse, distance to tongue anlage shorter than to medial end of ventral elum. *Ventral velum* continuous, with spicular support, highly wavy, margin with 25 projections forming a median notch medially. *Glottis* small. *Branchial baskets* oblique, longer than wide, 3 filter plates on each side, length of the second filter plate about 1/2 length of floor arena.

Natural history notes. These tadpoles were captured at night by hand in a small stream. They were seen remaining motionless near the water surface. When the collector came close, they immediately dived down to the bottom and hid under a rock (approximately 30 cm large). The tadpoles were caught by moving hands slowly under the rock. At night male frogs of *Quasipaa asciculispina* were calling sitting on the rocks. Several males and females were captured by

Fig. 4. Buccal floor of *Quasipaa fasciculispina* (based upon THNHM 13108.2, Gosner's stage 28). (a) general view, (b) anterior infralabial papillae, (c) posterolateral infralabial papillae, (d) buccal pocket area. Scale bar: 1 mm.

hand to observe external morphology and then released. In the same stream, only a few tadpoles of *Xenophrys* sp. were found. They probably belonged to *Xenophrys lekaguli* which was described from this locality by STUART et al. (2006), although other species of *Xenophrys*, such as *Xenophrys auralensis*, could occur in this region of Thailand. Several calls of *Philautus* sp. were heard along the stream banks.

DISCUSSION

OHLER & DUBOIS (2006) studied the phylogenetic relationships and the generic taxonomy of the tribe Paini and recognized six genera: *Allopaa* Ohler & Dubois, 2006, *Chaparana* Bourret, 1939, *Chrysopaa* Ohler & Dubois, 2006, *Gynandropaa* Dubois, 1992, *Nanorana*

Table 2. Diagnosis, size, KRF and bibliographic references of larvae of the genus *Quasipaa* Dubois, 1992. Data about the tadpoles of *Q. courtoisi*, *Q. jiulongensis*, *Q. tibetana* and *Q. yei* are missing as these tadpoles are not known.

Species	Gosner's stage	Total size (mm)	SVL (mm)	Larval diagnosis	KRF	References
Q. boulengeri	36-38	49.2-55.1	17.8-19.5	Dorsum yellow brown or light brown, tail light coloured with dark dots, a black transverse stripe between body and tail; tail end bluntly pointed, lower labial papillae in two rows	1:(3+3)-(4+4)/1+1:2	LIU, 1940, 1950; LIU & HU, 1961; WU et al., 1988; YANG, 1991; YE et al., 1993; FEI, 1999; FEI & YE, 200
Q. exilispinosa	28-36	54.1-60.9	18.2-20.5	Body pale yellow, tail with dark spots, tail end bluntly rounded, lower labial papillae in two rows	1:3+3/1+1:2	ANONYMOUS, 1975; FEI, 1999
Q. fasciculispina	28, 37	71.9, 77.7	30.6, 31.3	Large tadpole, body brown with dark dots, tail creamy brown with numerous black spots; tail tip subelliptical with slight point, lower labial papillae in three rows	2:5+5/1+1:2	INTHARA et al., 2005; this study
Q. robertingeri	not given	53	21	Dorsum brown yellow, tail light yellow or yellow, without spots, a brown transverse stripe between body and tail, no upper labial papillae, lower labial papillae arranged in two rows	1:4+4/1+1:2	FEI & YE, 2001
Q. shini	36-38	57.0-72.7	22.0-25.2	Body olive, 3-4 dark spots dorsolaterally on tail muscle; tail end bluntly pointed, lower labial papillae in two rows	1-2:(4+4)-(5+5)/1+1:1-2	LIU & HU, 1962; WU et al., 1988; YE et al., 1993; FEI, 1999
Q. spinosa	34-38	53.9-66.0	18.7-22	Body black gray, middle of back light coloured, tail with spots, tail end bluntly rounded, lower labial papillae in two rows	2:(3+3)-(4+4)/1+1:2	BOURRET, 1942; WU et al., 1988; YANG, 1991; YE et al., 1993; FEI, 1999
Q. verrucospinosa	27-29	71.1-75.4	–	Large tadpole, dorsum black brown greenish, tail heavily spotted, lower labial papillae in four rows	1:5+5/1+1:2; 2:4+4/1+1:2	BOURRET, 1942; INGER et al., 1999

ünther, 1896, and *Quasipaa* Dubois, 1992. *Quasipaa* comprises at present 11 species: *uasipaa boulengeri* (Günther, 1889); *Q. courtoisi* (Angel, 1922); *Q. exilispinosa* (Liu & Hu, 975); *Q. fasciculispina* (Inger, 1970), *Q. jiulongensis* (Huang & Liu, 1985); *Q. robertingeri* (Wu Zhao, 1995); *Q. shini* (Ahl, 1930); *Q. spinosa* (David, 1875); *Q. tibetana* (Boulenger, 1917); *verrucospinosa* (Bourret, 1937), and *Q. yei* (Chen, Qu & Jiang, 2002). The tadpoles of most f these species are known (table 2), but not those of the recently described ones or those with xonomic problems (i.e., *Q. courtoisi*, *Q. jiulongensis*, *Q. tibetana* and *Q. yei*), or *Q. fasciculispina*.

The larva of *Q. fasciculispina* is a large tadpole with creamy body background shaded by ark pigmentation, gray ventral side and creamy white tail with numerous black spots, and a RF 2:5+5/1+1:2. The tadpoles studied here are similar to those described by INTHARA et al. 2005). They resemble some other members of this genus which are usually of creamy or ellow brown coloration with black spots on body and tail. However, they differ from all other nown tadpoles of *Quasipaa* except *Q. verrucospinosa* by their large size: they are the second rgest of the known tadpoles of *Quasipaa* with a total length of 71.9 mm and 77.7 mm and body length of 24.0 mm and 23.9 mm at Gosner's stage 28 and 37, respectively. They differ lso from some of the other *Quasipaa* tadpoles by their KRF. Tadpoles of the genus *Quasipaa* ave from seven to ten keratodont rows, on the upper labium this number varies more than on e lower labium which normally has just three rows. The tadpole of *Q. fasciculispina* differs om the tadpoles of *Q. boulengeri*, *Q. exilispinosa* and *Q. robertingeri* in having two undivided ows of keratodonts on the upper labium (vs. just one in the latter species) and in having more divided rows (five vs. three or four). Some individuals of *Q. spinosa* have two undivided keratodonts rows on the upper labium but the number of divided rows in this species is lower than in *Q. fasciculispina* (three to four vs. five). *Quasipaa verrucospinosa* is the largest of the known tadpoles of the genus. Furthermore it can be distinguished of *Q. fasciculispinosa* by its lower keratodont row number on the upper labium (only six instead of seven in *Q. fasciculispina*) and four rows of papillae on the lower labium. The only species which can have a similar upper labium keratodont row number is *Quasipaa shini* (KRF 1:5+5/1+1:2, 2:5+5/1+1:1 or 2:4+4/1+1:1), but in this case the lower labium keratodont row number is only two. *Q. fasciculispina* is the only species of *Quasipaa* present in its area of distribution, no other *Quasipaa* species occurring in sympatry with it. The tadpoles of four species of *Quasipaa* are not yet known: *Q. courtoisi*, *Q. jiulongensis*, *Q. tibetana* and *Q. yei*. Total length, body length, KRF and a larval diagnosis of all known tadpoles of *Quasipaa* are summarized in table 2.

Although stated as closely related to *Q. verrucospinosa* in the original description (INGER, 1970), by its large size and its KRF the tadpole of *Q. fasciculispinosa* seems closer to that of *Q. shini*.

ACKNOWLEDGEMENTS

We are grateful to the Muséum national d'Histoire naturelle (MNHN, Paris, France) and the Thailand Natural History Museum (THNHM, Pathum Thani, Thailand) for facilitation of this study. Field work was in part supported by a grant of the Paris Museum (PPF "Etat et structure phylogenetique de la biodiversite actuelle et fossile"). CT and YC thank the Ministry of Science and Technology, Thailand for supporting PhD scholarships. Annemarie Ohler and Alain Dubois (MNHN, Paris) are thanked for their corrections and comments.

LITERATURE CITED

ANONYMOUS [Sichuan Provincial Institute of Biology and Sichuan Medical College], 1975 [September]. Report of three new species of Amphibia from Fujian province. *Acta zoologica sinica*, Beijing, **21** (3): 265-271, pl. 1. [In Chinese]. [Publication date: DUBOIS, 1979: 653].

ALTIG, R. & MCDIARMID, R. W., 1999. Body plan: development and morphology. *In*: R. W. MCDIARMID & R. ALTIG, (ed.), *Tadpoles: the biology of anuran larvae*, Chicago & London, The University of Chicago Press: 24-51.

BOURRET, R., 1942. *Les batraciens de l'Indochine*. Hanoi, Institut Océanographique: i-x + 1-547, 4 pl.

BRINGSOE, H., 2002. Herpetologische beobachtungen am Khao Soi Dao, Ost Thailand. 1. Der Stachelbrust-Riesenfrosch, *Paa fasciculispina* (Inger, 1970). *Sauria*, **24** (1): 9-16.

DUBOIS, A., 1976. Les grenouilles du sous-genre *Paa* du Nepal (famille Ranidae, genre *Rana*). *Cahiers népalais-Documents*, Paris, CNRS, **6**: i-vi + 1-275.

—— 1979. Notes sur la systematique et la repartition des Amphibiens Anoures de Chine et des regions avoisinantes. 1. *Rana exilispinosa* Liu & Hu, 1975 et *Rana (Paa) panaspinosa* Dubois, 1975. *Bull. Soc. linn. Lyon*, **48**: 649-656.

—— 1987. – Miscellanea taxinomica batrachologica (I). *Alytes*, "1986", **5** (1-2): 7-95.

—— 1992. Notes sur la classification des Ranidae (Amphibiens Anoures). *Bull. Soc. linn. Lyon*, **61** (10): 305-352.

----- 1995. Keratodont formulae in anuran tadpoles: proposals for a standardization. *J. zool. Syst. evol. Res.*, **33**: i-xv.

Fei, L., (ed.), 1999. *Atlas of amphibians of China*. Zhengzhou, Henan Press of Science and Technology: [i-ii] + 1-432. [In Chinese]

Fei, L. & Ye, C., 2001. *The colour handbook of the amphibians of Sichuan*. Chengdu, Chengdu Institute of Biology, "2000": [i-xv] + 1-263. [In Chinese] [Publication date according to printing date given in page ii]

Frost, D. R., Grant, T., Faivovich, J., Bain, R. H., Haas, A., Haddad, C. F. B., de Sa, R. O., Channing, A., Wilkinson, M., Donnellan, S. C., Raxworthy, C. J., Campbell, J. A., Blotto, B. L., Moler, P., Drewes, R. C., Nussbaum, R. A., Lynch, J. D., Green, D. M. & Wheeler, W. C., 2006. – The amphibian tree of life. *Bull. amer. Mus. nat. Hist.*, **297**: 1-370.

Gosner, K. L., 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, **16**: 183-190.

Grismer, L. L., Chav, T., Neang, T., Wood, P. L., Jr., Grismer, J. L., Youmans, T. M., Ponce, A., Daltry, J. C. & Kaiser, H., 2007. – The herpetofauna of the Phnom Aural Wildlife Sanctuary and checklist of the herpetofauna of the Cardamom mountains, Cambodia. *Hamadryad*, **31** (2): 216-241.

Grosjean, S., 2006. The choice of external morphological characters and developmental stages for tadpole-based anuran taxonomy: a case study in *Rana (Sylvirana) nigrovittata* (Blyth, 1855) (Amphibia, Anura, Ranidae). *Contr. Zool.*, **74** (1-2): 61-76.

Inger, R. F., 1970. A new species of frog of the genus *Rana* from Thailand. *Fieldiana Zool.*, **51** (14): 169-174.

Inger, R. F., Orlov, N. & Darevsky, I., 1999. - Frogs of Vietnam: a report on new collections. *Fieldiana Zool.*, (n.s.), **92**: 1-46.

Inthara, C., 2000. *Study on mouthparts structures in relation to feeding behavior of some tadpole species*. Master Thesis, Bangkok, Kasetsart University: 1-167. [In Thai with English Abstract]

Inthara, C., Laohachinda, V., Nabhitabhata, J., Chuaynkern, Y. & Kumtong, P., 2005. Mouth part structures and distribution of some tadpoles from Thailand. *Thailand nat. Hist. Mus. J.*, **1** (1): 55-78.

Jiang, J., Dubois, A., Ohler, A., Tillier, A., Chen, X., Xie, F. & M. Stöck, 2005. Phylogenetic relationships of the tribe Paini (Amphibia, Anura, Ranidae) based on partial sequences of mitochondrial 12S and 16S rRNA genes. *Zool. Sci.*, **22**: 353-362.

Khonsue, W. & Thirakhupt, K., 2001. A checklist of the amphibians in Thailand. *Nat. Hist. J. Chulalongkorn Univ.*, **1** (1): 69-82.

Laohachinda, V., Noikotr, K., Inthara, C. & Luangsakulpong, V., 2002. The diversity of anurans in Thailand. *In*: V. Baimai & R. Tantalakha (ed.), *BRT research reports 2002*, BRT Program, Bangkok, Chuan Printing Press Ltd Part: 203-211. [In Thai with English Abstract]

Liu, C.-C., 1940. Tadpoles of West China Salientia. *J. West China Border Res. Soc.*, (B), **12**: 7-55, 4 pl.

----- 1950. Amphibians of western China. *Fieldiana Zool. Mem.*, **2**: 1-400, pl. 1-10.

Liu, C. & Hu, S., 1961. *The tailless amphibians of China*. Beijing, Science Press: [i-ii] + i-xvi + 1-364, pl. 1-6 + 1-28. [In Chinese]

----- 1962. – A herpetological report of Kwangsi. *Acta zoologica sinica*, **14** (suppl.): 73-104. [In Chinese]

Nabhitabhata, J. & Chan-ard, T., 2005. *Thai Red Data: Mammals, Reptiles and Amphibians*. Bangkok, Office of Natural Resources and Environmental Policy and Planning: 1-234.

Nabhitabhata, J., Chan-ard, T. & Chuaynkern, Y., 2004. *Checklist of amphibians and reptiles in Thailand*. Bangkok, Office of Environmental Policy and Planning, "2000": 1-152.

Noikotr, K. & Lauhachinda, V., 2002. Diversity of anurans in Khaokitchakut, Chanthaburi Province. *J. Wildlife Thailand*, **10** (1): 7-16. [In Thai with English abstract].

Ohler, A. & Dubois, A., 2006. Phylogenetic relationships and generic taxonomic of the tribe Paini (Amphibia, Anura, Ranidae, Dicroglossinae), with diagnoses of two new genera. *Zoosystema*, **28** (3): 769-784.

Ohler, A., Swan, S. R. & Daltry, J. C., 2002. A recent survey of the amphibians fauna of the Cardamom Mountains, southwest Cambodia with descriptions of three new species. *Raffles Bull. Zool.*, **50**: 465-481.

STUART, B. L., CHUAYNKERN, Y., CHAN-ARD, T. & INGER, R. F., 2006. – Three new species of frogs and a new tadpole from eastern Thailand. *Fieldiana: Zool.*, (n.s.), **111**: 1-19.

STUART, B. L. & EMMETT, D. A., 2006. – A collection of amphibians and reptiles from the Cardamom Mountains, southwestern Cambodia. *Fieldiana: Zool.*, (n.s.), **109**: 1-27.

WU, L., DONG, Q. & XU, R., 1988. – *The amphibian fauna of Guizhou*. Guiyang, Guizhou People's Press: [i-vii] + 1-192, 1 pl. [In Chinese].

YANG, D. (ed.) 1991. – *The Amphibia fauna of Yunnan*. Kunming, China Forestry Publishing House: [i-vii] + i-iv + 1-259. [In Chinese].

YE, C., FEI, L., & HU, S., 1993. – *Rare and economic amphibians of China*. Chengdu, Sichuan Publishing House of Science and Technology. [i-iii] + 1-2 + 1-2 + 1-7 + 1-412. [In Chinese].

Corresponding editor: Alain DUBOIS.

Alytes, 2009, **26** (1-4): 97-116.

Two new species of the genus *Euphlyctis* (Anura, Ranidae) from southwestern India, revealed by molecular and morphological comparisons

S. Hareesh JOSHY *, Mohammad Shafiqul ALAM **, Atsushi KURABAYASHI **,
Masayuki SUMIDA ** & Mitsuru KURAMOTO ***

* Rondano Biodiversity Research Laboratory, St. Aloysius College, Mangalore 575 003, Karnataka, India

** Institute for Amphibian Biology, Graduate School of Science, Hiroshima University,
Higashihiroshima, Hiroshima 739-8526, Japan

3-6-15 Hikarigaoka, Munakata, Fukuoka 811-3403, Japan

Two new frog species of the genus *Euphlyctis*, which were shown to be two distinct taxa by mitochondrial DNA analyses, are described from Karnataka State, southwestern India. On the molecular phylogenetic tree, the first new species appears as a sister group with respect to *E. hexadactylus*. The second new species forms a group with *E. cyanophlyctis*. The first species differs from *E. hexadactylus* in having a distinctly smaller snout-vent length and dark brown bold markings on the dorsum, a smaller head, shorter hindlimbs and wider eyelids, relative to snout-vent length. The second species differs from the close relative *E. cyanophlyctis* in having shorter fingers. Its advertisement calls are composed of trills that are much longer in duration, are composed of more numerous pulses, and have a lower dominant frequency than those of *E. cyanophlyctis* and *E. hexadactylus*. Morphological comparisons between the four species are presented. The present study reveals hitherto overlooked cryptic biodiversity in the genus *Euphlyctis*.

INTRODUCTION

Euphlyctis is a small genus comprising only four currently recognized species *E. cyanophlyctis* (Schneider, 1799) from Iran, Afghanistan, Pakistan, Nepal, India, Sri Lanka, Malaya and Vietnam, *E. ehrenbergii* (Peters, 1863) from Saudi Arabia and Yemen; *E. ghoshi* (Chanda, 1991) from Manipur, India, and *E. hexadactylus* (Lesson, 1834) from India, Sri Lanka and Bangladesh (FROST, 1985; CHANDA, 1991, DUBOIS, 1992). *Euphlyctis cyanophlyctis* and *E. hexadactylus* are known to occur in southwestern India (BIJU, 2001; DANIELS, 2005). These species are aquatic or semi-aquatic frogs with wide toe webbing that usually live half-submerged in water, or on the water edge of ponds, wetlands, paddy fields and ditches.

In 2003, we collected small frogs of the genus *Euphlyctis* from Mangalore, together with *E. hexadactylus* and *E. cyanophlyctis*. At first, we considered the small ones as juveniles of *E. hexadactylus*. However, mtDNA data revealed that the small frogs were distinctly different from *E. hexadactylus* as well as from *E. cyanophlyctis* (Kurabayashi et al., 2005; Alam et al., 2008). We collected similar small *Euphlyctis* frogs from Mudigere in the Western Ghats in 2007, and the mtDNA data, described in the present study, clarified that the frogs from Mudigere differed from those of Mangalore. Alam et al. (2008) also demonstrated the presence of another cryptic *Euphlyctis* species from Bangladesh by mtDNA analysis, but the two new Indian taxa here treated were clearly different from that from Bangladesh. These latter two Indian frogs are described below as two new species.

Recently, many new anuran species have been described from southwestern India, including the Western Ghats (e.g., Dubois et al., 2001, Biju & Bossuyt, 2003, 2005, 2006, Kuramoto & Joshy, 2003; Biju et al., 2007; Kuramoto et al., 2007). This indicates that the wealth of amphibian biodiversity in this area is beyond the expectation generally recognized. The present study and other recently obtained evidence sheds light on the cryptic biodiversity in the small and rather unnoticed genus *Euphlyctis*.

MATERIAL AND METHODS

Euphlyctis frogs were collected from Adyar (12°52'N, 74°55'E, altitude 1 m) and Bajpe (12°58'N, 74°50'E; altitude ca. 70 m) in Mangalore, Dakshin Kannad District of Karnataka, and from Mudigere (13°07'N, 75°31'E, altitude ca. 1020 m), Chikumagalur District of Karnataka, during the rainy season (May to July), from 2003 to 2008. To elucidate the genetic divergence and phylogenetic relationship of the *Euphlyctis* taxa occurring in southwestern Karnataka, partial mtDNA portions corresponding to 12S and 16S rRNA genes were analyzed for 37 *Euphlyctis* samples involving those of *E. hexadactylus* from Adyar and *E. cyanophlyctis* from Bajpe, Padil (Mangalore), Karnoor (Dakshin Kannad District) and Madikeri (Kodagu District).

In the present study, the mtDNA fragments were newly amplified and sequenced for 14 specimens and the data of the remaining 23 taxa were obtained from our previous studies (Alam et al., 2008). The DNA amplification and sequence strategies followed the procedures as in the previous papers. The resultant sequences of each 12S and 16S rRNA gene were initially aligned using ClustalX 1.83 (Thompson et al., 1997), the initial 12S and 16S rRNA alignment data contained 566 and 520 nucleotide sites, respectively. From these alignment data, the genetic divergence (uncollected *p* value) between taxa was calculated. To perform sophisticated phylogenetic analyses, gaps and ambiguous alignment sites were excluded from the initial alignments using Gblocks 0.91b (Castresana, 2000). To check whether 12S and 16S rRNA data could be submitted to combined analyses, a permutation homology test (Farris et al., 1995) was conducted using PAUP* 4.10b (Swofford, 2001) ($P = 0.124$). Then, the two gene data were concatenated. The concatenated alignment data contained a total of 976 nucleotide sites, 192 of which were parsimoniously informative. Phylogenetic analyses based on the concatenated data were conducted sing maximum likelihood (ML) and Bayesian inference (BI) methods. In these analyses, *ejervarya limnocharis* (accession no AY158705; Liu et al, 2005) and *Limnonectes gianensis* (AY974191, Nie et al., unpublished) were used as outgroups. For ML and BI nalyses, appropriate substitution models were estimated using Akaike information riteria implemented in Modeltest 3.7 (Posada & Crandall, 1998), and a general me-reversible substitution model with gamma population and proportion of invariable tes sub-models (GTR+G+I) was chosen. ML analysis was performed using PAUP* onparametric bootstrap (BP) values under ML were calculated with 300 replicates. BI nalysis was performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). The following settings were also used for the BI analysis number of Markov chain Monte Carlo enerations = 15 × 10^5 and sampling frequency = 10 The burn-in size was determined by hecking convergences of log likelihood ($\ln L$) values, and the first 1 × 10^5 generations were iscarded. The statistical support of the resultant BI tree was evaluated by Bayesian posterior robabilities (BPP)

Measurements were recorded for snout-vent length (SVL), head length (HL), head width HW), snout to nostril distance (S-N), inter-nostril distance (N-N), nostril to eye distance N-E), eye diameter (ED), inter-orbital distance (E-E), eyelid width (ELW), tympanum iameter (TD), hand length (HAL), no. 1 to no. 4 finger length (F1-F4), hindlimb length HLL), femur length (FEL), tibia length (TIL), foot length (FOL), and no. 1 to no 5 toe ength (T1-T5). For details of the method of measurements see Kuramoto & Joshy (2006) nd Kuramoto et al. (2007) Juvenile specimens were excluded from measurements. For norphological comparison, we measured six preserved specimens of *E. hexadactylus* from Adyar, Mangalore and 19 specimens of *E. cyanophlyctis* from Mangalore, Karnoor, Bhatkal, alagini, Mudigere and Madikeri, all in Karnataka State (see fig. 1 in Kuramoto et al , 2007), leposited in the Rondano Biodiversity Research Laboratory. St. Aloysius College. Examined pecimens are listed below except for those of the new species. Discriminant analyses were erformed by SPSS (15 0J) statistics software (SPSS Japan, Inc.) using the measurements vithout any transformation.

Euphlyctis cyanophlyctis. Bajpe. RBRL 04070611, 05072202, 07072114 (1 adult ♂, adult ♀). Bhatkal: RBRL 00062601-00062603, 00062605-00062607 (6 adult ♀). Karnoor. RBRL 01080508, 04071139, 04071140 (2 adult ♂, 1 adult ♀). Madikeri: RBRL 03060702 1 adult ♀) Mudigere RBRL 05070921, 05070922 (1 adult ♂, 1 adult ♀) Padil: RBRL 3052303 (1 adult ♀) Talagini RBRL 01081113, 01081114, 01081118 (3 adult ♀)

Euphlyctis hexadactylus Adyar RBRL 03060601, 05071901-05071903, 07072801, 7072802 (5 adult ♂, 1 adult ♀).

The advertisement calls were recorded in Mudigere on 29 July 2007 at an air temperature f 23.2°C and on 27 July 2008 at 21 0°C using an MD recorder (Sony MZ-B10) The recorded alls were analyzed by Avisoft-SASLab Light software (Avisoft Bioacoustics)

The type specimens were deposited in the Natural History Collections of the Bombay Natural History Society (BNHS), and the other specimens were stored in the Rondano Biodiversity Research Laboratory, St. Aloysius College (RBRL).

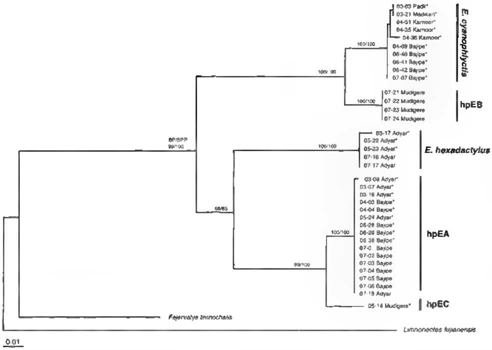


Fig. 1. - Phylogenetic relationships of *Euphlyctis* taxa from Karnataka, India, inferred from mitochondrial 12S and 16S rRNA gene data. Maximum likelihood tree (−ln*L* = 3356.93) is represented here. Bayesian analysis reconstructed the same tree topology. The numbers on the nodes are BP in ML and BPP in BI. Three haplotype groups are shown by abbreviations, hpEA, hpEB and hpEC. Field numbers of samples and collecting sites are shown. Asterisks indicate that the samples were used in analyses by KURABAYASHI et al. (2005) and ALAM et al. (2008).

RESULTS

MOLECULAR PHYLOGENY AND GENETIC DIVERGENCE OF THE *EUPHLYCTIS* TAXA FROM KARNATAKA

Based on the 12S and 16S rRNA gene sequences, the Indian *Euphlyctis* specimens consisted of five major haplotype groups (fig. 1). Two of the five groups corresponded to *E. cyanophlyctis* and *E. hexadactylus*, and the others were temporarily named as hpEA, hpEB and hpEC. In the ML tree (fig. 1), the hpEB group formed a group with *E. cyanophlyctis* and this clade was strongly supported by statistical values (BP = 100; BPP = 100). The hpEA and hpEC groups formed a group, and they became a sister taxon with respect to *E. hexadactylus*, but statistical support for this relationship was not high (BP = 68, BPP = 85). The same relationships as for the five major *Euphlyctis* taxa were also reconstructed in our Bayesian analysis. Furthermore, the present result was partially congruent with the results of previous studies. KURABAYASHI et al. (2005) showed that small-sized *Euphlyctis* specimens (hpEA) rom Mangalore (Adyar and Bajpe) differed genetically from *E. hexadactylus*, and ALAM et al. 2008) found that one specimen from Mudigere (hpEC) was closely related to the hpEA roup, but there was a degree of genetic divergence between the groups.

According to ALAM et al. (2008), the average sequence divergences between *E. hexadactylus* and hpEA (Ehex-In1 and Ehex-In2 in ALAM et al., 2008) were 11.9 % and 6.3 % for 12S nd 16S rRNA genes, respectively. Because these values were larger than those previously eported from intraspecific sequence comparisons in mantellids (VENCES et al., 2005) and outh American bufonids and hylids (FOUQUET et al., 2007), ALAM et al. (2008) concluded hat the two haplotype groups should be separated taxonomically as different species. When e recalculated the average sequence divergence between these taxa with the present additionl material, the values were 13.0 % and 9.1 % for 12S and 16S rRNA genes, respectively. The pecimen from Mudigere collected in 2003 (hpEC, Ehex-In3 in ALAM et al., 2008) was also eparated clearly from *E. hexadactylus* (15.3 % and 9.1 % for 12S and 16S), but the sequence ivergence values (5.0 % and 2.3 %) did not support the distinct separation between the hpEC nd hpEA groups. Only one specimen with the hpEC haplotype has been found so far, and his specimen was apparently subadult. Thus, more specimens are needed before discussing its axonomic status.

The most remarkable finding in the present study was that the five specimens from Mudigere (hpEB) collected in 2007 formed a sister group to that of *E. cyanophlyctis* (fig. 1). Molecular divergence between hpEB and *E. cyanophlyctis* was 16.4 % for 12S and 10.7 % for 6S rRNA genes. As in the case between hpEA and *E. hexadactylus*, these values were large nough to regard the hpEB group as a distinct species from *E. cyanophlyctis*.

Our molecular analyses have revealed the occurrence of two undescribed species in outhwestern part of Karnataka. As discussed in the later section, the two haplotype (hpEA nd hpEB) groups were morphologically distinct from *E. hexadactylus* and *E. cyanophlyctis*, espectively, and from each other. These indicate that the two haplotype groups are reproductively distinct, and are described below as new species.

TAXONOMY

Euphlyctis aloysii sp. nov.

(fig. 2-3)

hpEA group in fig. 1 and in KURABAYASHI et al. (2005).
Ehex-In2 group in ALAM et al. (2008).

Diagnosis. — Small *Euphlyctis* species, SVL from 31.8 to 45.2 mm in females. It differs from *E. hexadactylus* in its distinctly smaller body size, having four large elliptical dark markings on the dorsum, smaller head, shorter hindlimbs, and wider eyelids, relative to SVL. The presence of large dorsal markings and thin mid-dorsal stripe readily distinguishes this species from *E. cyanophlyctis*. The eyes and tympanums are smaller, and femur and tibia are shorter, relative to SVL, in *E. aloysii* than in *E. cyanophlyctis*.

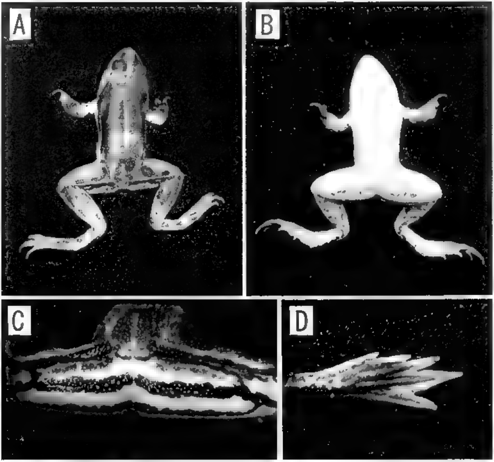


Fig. 2. Holotype of *Euphlyctis aloysii* sp. nov. (BNHS 5123, ♀ from Bajpe). Dorsal view (A), ventral view (B), posterior aspect of thigh (C), and foot (D). Lower part of abdomen was cut open for sexing, and the opening is seen in B.

Holotype. BNHS 5123 (fig. 2), female, SVL 40.4 mm, collected in Bajpe, Mangalore, on 21 July 2007.

Paratypes. BNHS 5124, ♀, SVL 38.6 mm, Adyar, Mangalore, 6 June 2003. BNHS 5125, ♀, SVL 37.1 mm, Bajpe, Mangalore, 21 July 2007. BNHS 5126, ♀, SVL 37.2 mm, Adyar, Mangalore, 28 July 2007.

Other specimens examined. RBRL 03052501, 05071904, two adult ♀, Adyar. RBRL 04070601-04070603, 06072003-06072004, 06072404, 07072101, 07072104-07072113, 07072115, 18 adult ♀, Bajpe.

Description of holotype (measurements in mm). Vomerine teeth round, situated near anterior end of upper jaw; tongue tip bifurcated.

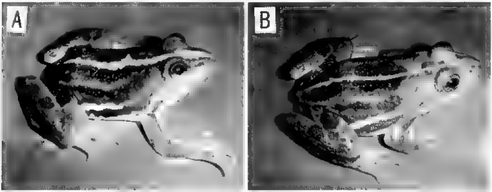


Fig. 3 *Euphlyctis aloysii* sp. nov. RBRL 06072004 (A) and RBRL 06072404 (B), showing coloration in life.

Head small, wider than long (HL 12.4, HW 13.1); snout slightly pointed; nostril nearer to tip of snout than to eye (S-N 2.9, N-E 3.1), loreal region concave, canthus rostralis blunt; internarial distance larger than inter-orbital, the latter smaller than eyelid width (N-N 2.4, E-E 1.4, ELW 3.3); tympanum large, about 75 % of eye diameter (ED 4.2, TD 3.3).

Finger free, finger tip small, slightly pointed; first finger longer than second (F1 7.0, F2 4.5); subarticular tubercle moderate; finger lengths F2 < F4 < F1<F3 (F3 7.2, F4 4.7).

Distal part of thigh thick; tibio-tarsal articulation slightly apart when legs folded at right angle to body axis, foot length larger than femur length and slightly larger than tibia length (FOL 19.1, FEL 18.4, TIL 19.0); toe tip small, slightly pointed; subarticular tubercle moderate, toe lengths T1 < T2 < T3 < T5 < T4 (T1 7.1, T2 9.9, T3 11.8, T4 15.6, T5 13.4); web nearly reaching toe tip and sharply incised (fig. 2D); inner metatarsal tubercle indistinct.

Supra-tympanic fold thin, forming granular row at posterior part of tympanum, not reaching arm base, numerous small round ridges on dorsum, no ridges on flank and thigh, underside smooth, except a pair of rows consisting of a series of small dermal projections from the anterior edge of forelimbs to groin

In preservative, dark brown above with a thin mid-dorsal stripe, small black spots from beneath eye to forelimb base; large dark brown elliptical or round markings on dorsal side of thigh and shank, wide white longitudinal stripe on sides from above forelimb to groin; three dark brown longitudinal stripes and intervening two white stripes on posterior side of thigh (fig. 2C); thin pale stripe on outer edge of shank, dark streak from ankle to outer edge of foot; ventral side white; irregular dark line pattern on underside of thigh (fig. 2B); irregular dark markings on underside of shank.

Color in life Dorsum light brown with a thin greenish mid-dorsal stripe, and green patches over upper jaw and from eyelid to shoulder, two pairs of rather conspicuous large elliptical markings on dorsum (fig. 3). At night, the dorsum was darker, and green color and dorsal markings became inconspicuous.

Variation. – Measurements for 24 female specimens are given in tab. 1. Of 24 specimens, 22 had a thin mid-dorsal stripe (fig. 3B), one had a relatively thick mid-dorsal stripe (fig. 3A), and only one (paratype BNHS 5124) lacked mid-dorsal stripe. Irregular line pattern on underside of thigh and shank differed from specimen to specimen, and extended to lower part of abdomen in some specimens. Paratype BNHS 5124 showed a distinct black dot line system composed of black horny tubercles; a curved dot line between anterior edge of foreleg, a pair of dot lines on both sides of the throat, a pair of dotted lines from the anterior part of the arm base, circling the upper edge of arm base, extending toward groin, then toward back; a pair of faint longitudinal black dotted lines on both sides of the venter. A similar dotted line system was reported in *E. cyanophlyctis* from Sri Lanka (Dutta & Manamendra-Arachchi, 1996), and one of the authors (MK) observed it in a preserved specimen of *E. hexadactylus* from Malabar (deposited in Muséum national d'Histoire naturelle, Paris: MNHN 1292.9, SVL 69.2 mm). These systems apparently represent the lateral line system (see Dubois & Ohler, 2001).

We did not observe juveniles of *E. hexadactylus*. The juveniles were described as "beautifully striped" (Boulenger, 1890), "have bars or spots of dark green and black on the back" (Daniel, 2002), or "more strikingly colored with patches of green and black scattered over the olive-black back" (Daniels, 2005). These descriptions fit the coloration of *E. aloysii* fairly well. Although precise comparisons wait for future studies, there may be a possibility that *E. aloysii* has been confused with juveniles of *E. hexadactylus* in some cases. The juveniles of *Hoplobatrachus tigerinus* have a beautiful green and black dorsal pattern, but they can be readily distinguishable from *E. aloysii* by the presence of many longitudinal dermal ridges on the back.

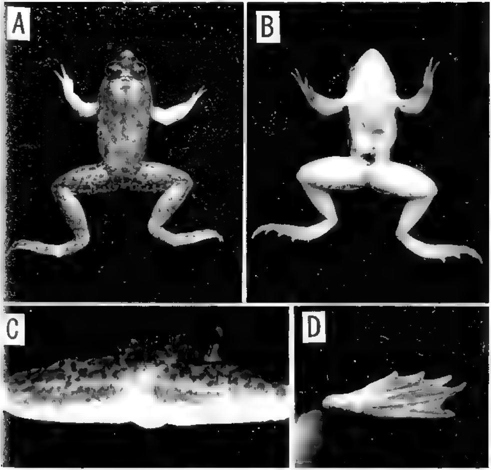
Our specimens were all females, and male sexual characters are unknown.

Ecology. – Females had mature ova in the ovaries. The ova are pigmented and ca. 1 mm in diameter. Since the gravid females were collected from late May to late July, spawning may begin in early August. During July, in the middle of the rainy season in Karnataka, we heard advertisement calls of *E. hexadactylus*, *Fejervarya caperata* Kuramoto et al., 2007 and *Hylarana aurantiaca* (Boulenger, 1904) in Adyar and those of *Fejervarya caperata*, *F. sahyadris* (Dubois et al., 2001), *Microhyla ornata* (Dumeril & Bibron, 1841) and *Polypedates maculatus* (Gray, 1830) in Bajpe, but we could not hear the calls of *E. aloysii*. Our specimens ($n = 24$) were composed of females only. The reason why males did not appear during our collecting was not clear.

Distribution. – Presently known only from Adyar and Bajpe in Mangalore. The hpEC group from Mudigere, which apparently relates to *E. aloysii* from external morphology and molecular analysis, may suggest the presence of a montane subspecies.

Etymology. – This species and the College where the main part of this study was carried out, were both named in honor of Aloysius Gonzaga (1568-1591). Aloysius was a Prince in Italy who entered a Jesuit order and died serving the plague-stricken people of Rome.

DNA sequence data for holotype. – Accession numbers are AB273171 and AB272606 for mitochondrial 12S and 16S rRNA genes, respectively (07-02 in fig. 1).



ig. 4 Holotype of *Euphlyctis mudigere* sp. nov. (BNHS 5127, ♂ from Mudigere). Dorsal view (A), ventral view (B), posterior aspect of thigh (C), and foot (D). Opening for removing tissue for DNA analysis is seen in B.

Euphlyctis mudigere sp. nov.
(fig. 4-6)

pEB group in fig. 1

iagnosis. Small *Euphlyctis* species with SVL from 28.1 to 34.8 mm in males. It differs from *hexadactylus* and *E. aloysii* in having a simple stripe pattern on the posterior side of the high and a bluntly incised web. The fingers, relative to SVL, are shorter than in *E. cyanophlyc-is*. The advertisement calls are 1.3 s in mean duration, and consist of about 16 pulses with the ominant frequency band at about 1.5 kHz. The calls differ from those of *E. cyanophlyctis* nd *E. hexadactylus*: call length longer, more numerous pulses in a call and lower dominant equency band.

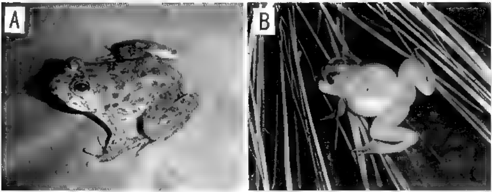


Fig. 5. – *Euphlyctis mudigere* sp. nov. Paratype (BNHS 5130) (A) and RBRL 08072504 (B), showing coloration in life.

Holotype. - BNHS 5127 (fig. 4), male, SVL: 31.1 mm, collected in Mudigere, on 29 July 2007.

Paratypes. – BNHS 5128, ♂, SVL 29.2 mm, Mudigere, 29 July 2007. BNHS 5129, ♂, SVL 28.1 mm, Mudigere, 29 July 2007. BNHS 5130 (fig. 5A), ♂, SVL 32.7 mm, Mudigere, 29 July 2007.

Other specimens examined. RBRL 07072905, 08072504 (fig. 5B), 08072505, three ♂, Mudigere.

Description of holotype (measurements in mm). Vomerine teeth round, situated near anterior end of upper jaw, tongue tip bifurcated.

Head small, wider than long (HL 10.3, HW 11.3); snout slightly pointed; nostril nearer to eye than to tip of snout (S-N 3.0, N-E 2.6); loreal region concave, canthus rostralis blunt; internarial distance larger than inter-orbital, the latter smaller than eyelid width (N-N 2.1, E-E 1.2, ELW 2.3); tympanum large, about 85 % of eye diameter (ED 3.8, TD 3.3).

Fingers free, gradually tapering to pointed tip; first finger larger than second (F1 4.6, F2 3.9), subarticular tubercle small; finger lengths F4 < F2 < F1 < F3 (F3 5.6, F4, 3.5). No thickening of the first finger, corresponding to nuptial pad, was noticed.

Distal part of thigh thick, tibio-tarsal articulation slightly apart when legs folded at right angle to body axis, femur length larger than tibia length, the latter larger than foot length (FEL 15.6, TIL 14.2, FOL 13.8), toe tip small, slightly pointed; subarticular tubercle small; toe lengths T1 < T2 < T5 < T3 < T4 (T1 5.1, T2 7.4, T3 10.3, T4 11.5, T5 10.1), web large, nearly reaching toe tip and bluntly incised (fig. 4D), inner metatarsal tubercle indistinct.

Dorsal surface with small tubercles; supra-tympanic fold present, but not distinct, underside smooth. A pair of vocal sacs on both sides of lower jaw near jaw angle.

In preservative, dorsum dark brown with indistinct small patches, irregular markings on upper side of hindlimb, a conspicuous white band on posterior side of thigh, accompanied with a thin black stripe on ventro-posterior side (fig. 4C), no mid-dorsal stripe, underside immaculate, vocal sacs light gray.

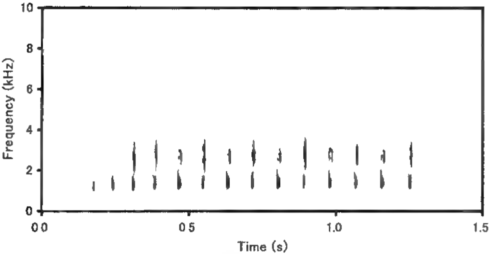


Fig. 6. – Sound spectrogram of the advertisement call of *E. mudigere* sp. nov. (FlatTop window, 323 Hz bandwidth).

Color in life. – Dorsum was light brown with many small darker patches (fig. 5A). In the night, these patches tended to fade (fig. 5B).

Variation. – Measurements for seven male specimens are given in tab. 1. None of the specimens had a mid-dorsal stripe. In external morphology, no distinct intra-specific variation was noticed. Because only male specimens were available, sexual variation is not known.

Advertisement calls. – The advertisement calls of *E. mudigere* recorded on 29 July 2007 at 23.2°C (fig. 6) were trills composed of 16.39 ± 2.77 pulses ($n = 18$, range 11 – 22), with total length of 1.31 ± 0.22 s (0.84 – 1.71 s). Pulse repetition rate was 11.71 ± 0.56 pulse/s. Frequencies were rather continuous from 1 to over 8 kHz. The dominant and fundamental frequency was at about 1.5 kHz and a second harmonics band was noticed at about 3 kHz. The calls recorded on 27 July 2008 at 21.0°C were nearly the same in number of pulses (16.36 ± 1.92 pulses, range 12 – 20, $n = 22$), but the call length was longer (1.48 ± 0.21 s, range 1.05 - 1.92 s) and the pulse repetition rate was lower (11.10 ± 0.32 pulse/s) than the calls recorded in 2007. The differences between the two recordings in call length and pulse repetition rate were slight, but statistically significant ($t = 2.428$ and $P = 0.020$ for call length; $t = 4.317$ and $P = 0.0001$ for pulse repetition rate). Because the call length became shorter and pulse repetition rate became higher with increasing temperatures (e.g. KURAMOTO & JOSHY, 2006), these may be due to the slight difference in air temperature at the time of recordings.

The advertisement calls of *E. cyanophlyctis* and *E. hexadactylus* were analyzed by KURAMOTO & JOSHY (in press). The calls of *E. mudigere* differed from the calls of *E. cyanophlyctis* which were not the trills but typically composed of a series of two-pulse notes. Compared with the calls of *E. mudigere*, the calls of *E. hexadactylus* were shorter in call duration (0.25 ± 0.07 s), fewer in pulse number (5.0 ± 1.18) and higher in dominant frequency (2.29 – 2.43 kHz).

Table 1. – Mean (x), standard deviation (s) and range in measurements (in mm) of four *Euphlyctis* species from Karnataka, India. See text for character abbreviations.

Measurement	*E. aloysii*		*E. mudigere*		*E. cyanophlyctis*				*E. hexadactylus*		
	Females (n = 24)		Males (n = [illegible])		Females (n = 15)		Males (n = 4)		Female	Male (n = 5)	
	x ± s	min – max	x ± s	min – max	x ± s	min – max	x ± s	min – max	(n = 1)	x ± s	min – max
SVL	37.58 ± 3. 5	31.8 – 45.2	31.2 ± 2.25	28.1 – 34.8	42.30 ± 7.01	33.0 – 56.9	35.10 ± 3.43	30.9 – 38.1	88.5	62.70 ± 4.32	56.0 – 67.7
HL	10.85 ± 0.98	9.2 – 12.5	9.53 ± 1.27	7.8 – 11.2	13.09 ± 2. 2	10.8 – 18.1	1 .08 ± 13	9.6 – 12.1	28.7	22. 4 ± 2.88	19.4 – 25.4
HW	12.38 ± 1.00	10.8 – 14.3	11.2 ± 0.88	10.3 – 12.2	14.23 ± 2.81	11.2 – 20.0	12.00 ± 1.30	10.7 – 13.4	31.1	22.30 ± 1.72	20.0 – 24.5
S-N	2.40 ± 0.36	8 – 3.4	2.43 ± 0.71	1.5 – 3.3	3. 5 ± 0.66	2.0 – 4.2	2.53 ± 0.61	9 – 3.3	5.7	5.26 ± 0.59	4.5 – 5.9
N-N	2.47 ± 0.30	2.0 – 3.1	2.19 ± 0.20	1.9 – 2.5	2.45 ± 0.49	1.7 – 3.6	2.58 ± 0.25	2.1 – 2.7	3.5	3.26 ± 0.1	3.1 – 3.4
N-E	2.64 ± 0.37	1.9 – 3.7	2.49 ± 0.94	1.6 – 4.2	3.45 ± 0.68	2.3 – 5.0	2.45 ± 0.72	1.8 – 3.3	8.5	5.74 ± 0.42	5.1 – 6.2
ED	3.86 ± 0.56	2.3 – 5.0	3.86 ± 0.74	2.5 – 4.9	5.24 ± 0.89	3.9 – 6.6	4.65 ± 0.52	3.9 – 5.0	7.7	7. 8 ± 0.66	6.2 – 8.0
E-E	1.62 ± 0.29	1.2 – 2.3	1.49 ± 0.25	1.2 – 1.9	1.83 ± 0.45	1. – 2.6	2.00 ± 1.48	1.0 – 4.2	3.4	2. 8 ± 0.48	5 – 2.8
ELW	2.50 ± 0.29	1.9 – 3.3	2.1 ± 0.34	1.4 – 2.5	2.69 ± 0.68	2.0 – 4.3	2.20 ± 0.48	1.4 – 2.8	4.8	3.52 ± 0.54	3.0 – 4.
TD	3.45 ± 0.50	2.6 – 4.5	3.0 ± 0.89	1.4 – 4.0	4.63 ± 0.82	3.3 – 5.9	4.15 ± 0.74	3. – 4.8	6.6	6.26 ± 0.63	5.5 – 7.2
HAL	9.04 ± 0.96	6.3 – 10.8	6.97 ± .86	5.0 – 9.5	10.90 ± .78	8.6 – 14.7	9.58 ± 0.60	9.0 – 10.4	14.6	14.52 ± 1.15	13.3 – 16.4
F1	5.49 ± 1.00	4.2 – 7.4	4.83 ± 0.87	3.8 – 6.1	8.29 ± .61	6.4 – 11.9	6.65 ± 0.93	5.5 – 7.5	13.6	9.78 ± 1.	8.2 – 11.6
F2	4.52 ± 0.53	3.5 – 5.6	3.89 ± 0.58	3.0 – 4.6	6. 8 ± . 7	4. – 8.	6.08 ± 1.19	5.1 – 7.8	15.9	8.44 ± 0.82	7.8 – 9.8
F3	6.44 ± 0.78	4.6 – 7.7	5.79 ± 0.68	4.8 – 6.9	7.71 ± .33	6.0 – 10.5	6.93 ± 0.70	6.0 – 7.6	17.1	1 .38 ± 1.03	9.9 – 12.7
F4	4.42 ± .47	4. – 5.8	4. ± 0.82	2. – 5.4	5.7 ± .08	4. – 7.0	5.58 ± .40	4.4 – 7.4	[illegible]	9.51 ± .47	8. – [illegible]
HLL	52.95 ± 5.09	44.7 – 64.7	45.06 ± 4.56	38.4 – 52.9	60.83 ± 8.88	49.8 – 80.0	52.10 ± 5.46	44.3 – 57.0	35.0	93.52 ± 2.93	79.7 – 99.6
FEL	6.48 ± 1.41	14.4 – 19.7	5.49 ± .02	13.8 – 17.0	20.71 ± 3. 8	16.8 – 25.9	16.70 ± 0.57	16.3 – 17.5	45.9	28.06 ± 3.44	23.0 – 32.4
TL	[illegible] ± 1.65	4 – [illegible]	5.90 ± .41	3.5 – [illegible]	21.69 ± [illegible]	6.5 – [illegible]	[illegible] ± .05	6. – 9.	47.9	.0.02 ± [illegible]	6. – 3.0
FOL	18.24 ± 1.40	14.0 – 20.4	14.74 ± .02	13.7 – 16.3	20.03 ± 3.09	14.4 – 25.4	17.23 ± 0.94	15.9 – 17.9	41.4	.70 ± .12	26.9 – 35.
T1	6.49 ± 0.85	5.1 – 9.3	5.3 ± 0.90	4.4 – 7.1	7.46 ± .85	4.0 – 10.9	6.71 ± 1.42	5.4 – 8.7	15.8	12.7 ± 1.64	0 – 4.9
T2	.81 ± 0.76	5 – 0.7	7.40 ± 0.91	6. – 9.7	0.4 ± .06	7.4 – 3.8	8.98 ± 2.36	2. – 7.3	20.4	15.96 ± 1.93	2.9 – [illegible]
T3	.97 ± 1.4	8 – 3.9	.24 ± 0.92	9.4 – 2.7	1.0 ± .70	3 – 9.7	2.25 ± .46	0.4 – 5.0	47.5	.76 ± 2.07	8.6 – 23.4
T4	4.65 ± 1.24	1.9 – 17.3	1 .86 ± .5	0.8 – 4.2	16.73 ± 3. 1	12 – 22.0	14.03 ± 1.39	2.8 – 6.0	36.0	26.46 ± .50	22.5 – 3
T5	12.30 ± 1.21	10.3 – 14.5	10.20 ± 0.94	9.3 – 12.2	14. 4 ± 2.44	10.2 – 19.2	12.50 ± 1.34	11.3 – 3.9	29.7	19.38 ± .8	0.8 – [illegible]

Ecology. Males were calling while floating among rice plants (fig. 5B). The calling males were observed in the middle portion of paddy fields without exception. On the banks of the same paddy fields, *Fejervarya granosa* Kuramoto et al., 2007 and *F. caperata* were actively calling. We could not collect females in paddy fields where males were calling.

Distribution. Presently known only from the type locality, Mudigere.

Etymology. Specific name was derived from the name of type locality, Mudigere. It is an invariable name in apposition to the generic name.

DNA sequence data for holotype. Accession numbers are AB377110 and AB377109 for mitochondrial 12S and 16S rRNA genes, respectively (07-21 in fig. 1).

MORPHOLOGICAL COMPARISONS BETWEEN *EUPHLYCTIS* TAXA FROM KARNATAKA

As shown in tab. 1, *Euphlyctis aloysii* and *E. mudigere* are distinctly smaller than *E. hexadactylus*. Ranges of SVL of *E. aloysii* females and *E. mudigere* males do not overlap with those of *E. hexadactylus*. The snout-vent length of *E. aloysii* females is significantly smaller than that of *E. cyanophlyctis* females ($U = 107$, $P = 0.035$), whereas no significant difference was obtained between males of *E. mudigere* and *E. cyanophlyctis* ($U = 5$, $P = 0.089$). Fairly distinct large dark blotches on the dorsum of female *E. aloysii* were not observed in

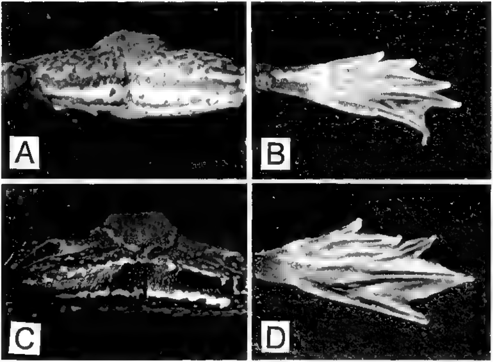


Fig. 7. Posterior side of thigh and foot of *E. cyanophlyctis* (RBRL 05070921, ♀ from Mudigere) (A, B) and those of *E. hexadactylus* (RBRL 06071903, ♂ from Adyar) (C, D)

E. hexadactylus and *E. cyanophlyctis*. Vomerine teeth of *E. hexadactylus* are distinct, forming two highly elevated oblique lines between choanae. In *E. cyanophlyctis*, subarticular tubercles are distinct in contrast to the indistinct tubercles of *E. aloysii* and *E. mudigere*. The mid-dorsal stripe is absent in *E. mudigere* and *E. cyanophlyctis*.

As a whole, *E. aloysii* and *E. mudigere* resemble *E. hexadactylus* and *E. cyanophlyctis*, respectively. However, large dark brown markings like those on the dorsum of *E. aloysii* were never observed in *E. hexadactylus* or any other *Euphlyctis* species. These markings were very conspicuous in specimens which died accidentally during transportation (RBRL 04070601, 04070602). The stripe pattern on the posterior side of the thigh of *E. hexadactylus* differs from that of *E. aloysii* consisting of two thinner white stripes and a much thicker black stripe between the two white stripes (fig. 7C). The web of *E. hexadactylus* is sharply incised as in *E. aloysii* (fig. 7D). The thigh stripe pattern of *E. mudigere* is similar to that of *E. cyanophlyctis* (fig. 7A), and the web is not deeply incised in both species (fig. 7B). The dorsal surface is densely covered with small granular tubercles in *E. cyanophlyctis*, whereas the granules are rather scarce in *E. mudigere*.

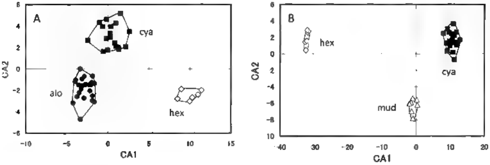
Euphlyctis aloysii was separated clearly from *E. hexadactylus* and *E. cyanophlyctis* by canonical discriminant analysis using measurements (fig. 8A). The statistics for discriminant

Table 2. – Statistics obtained from the discriminant analyses using measurements of five *Euphlyctis* species. Abbreviations: *alo*, *E. aloysii*; *cya*, *E. cyanophlyctis*; *ehr*, *E. ehrenbergii*; *hex*, *E. hexadactylus*; *mud*, *E. mudigere*.

Species compared	Number of variables	Eigenvalue			Wilks' lambda (*P*)			Discriminant result (%)	Figure
		Function 1	Function 2	Function 3	Function 1 (or 1-2, 1-3)	Function 2 (or 2-3)	Function 3		
alo, *cya*, *hex*	24	17 277	6.448	-	0 007 (< 0 001)	0 .34 (< 0 001)	--	100	8A
mud, *cya*, *hex*	24	285 730	12 187	--	0 000 (< 0 001)	0 076 (0.004)	--	100	8B
alo, *mud*	24	54.045	--	--	0 0.8 (< 0 001)	--	--	100	9A
alo, *mud*, *cya*, *hex*	24	14 013	5 147	1.888	0.004 (< 0 001)	0 056 (< 0 00)	0 346 (0 004)	100	9B
ehr, *cya*, *hex*	18	23.108	5..87	--	0 007 (< 0 001)	0 162 (0.034)	--	100	10A
ehr, *cya*, *hex*	14	15.105	3.311		0 0 4 (< 0 001)	0 232 (0 025)	--	100	10B

Table 3. – Mean, standard deviation and range in body ratios of four *Euphlyctis* species from southwestern Karnataka, India. See text for character abbreviations.

Ratio	*E. aloysii* (n = 24)			*E. mudigere* (n = [illegible])			*E. cyanophlyctis* (n = 19)			*E. hexadactylus* (n = 6)		
	x̄ ± s	min	max	x̄ ± s	min	max	x̄ ± s	min	max	x̄ ± s	min	max
HL/SVL	0.289 ± 0.020	0.252	0.331	0.30[illegible] ± 0.034	0.261	0.348	0.3[illegible]5 ± 0.02	0.288	0.388	0.348 ± 0.030	0.307	0.385
HW/SVL	[illegible]	[illegible]	[illegible]368	[illegible]	0.341	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]334	[illegible]
[illegible]/SVL	[illegible]	0.108	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]/SVL	0.066 ± 0.006	0.057	0.075	0.069 ± 0.005	0.063	0.078	0.061 ± 0.0[illegible]0	0.047	0.080	[illegible]50 ± 0.006	0.040	0.055
[illegible]/SVL	[illegible] ± 0.008	0.065	0.094	0.078 ± 0.026	0.051	0.[illegible]21	0.080 ± 0.0[illegible]3	0.056	0.1[illegible]	0.092 ± 0.004	0.087	0.09[illegible]
[illegible]/SVL	[illegible] ± 0.0[illegible]3	0.063	0.130	0.127 ± 0.023	0.078	0.[illegible]47	0.[illegible]28 ± 0.019	0.[illegible]02	0.185	[illegible] ± 0.0[illegible]2	0.087	0.119
E/SVL	[illegible] ± 0.009	[illegible]	0.069	0.047 ± 0.007	0.037	0.055	0.046 ± 0.0[illegible]8	0.03[illegible]	0.[illegible]	0.035 ± 0.005	0.027	0.041
[illegible]/SVL	[illegible]	[illegible]107	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]185	[illegible]	[illegible]	[illegible]164
TD/SVL	0.092 ± 0.0[illegible]3	0.066	0.1[illegible]7	0.095 ± 0.026	0.045	0.[illegible]22	0.[illegible]3 ± 0.01	0.087	0.[illegible]34	0.096 ± 0.0[illegible]4	0.075	0.113
HA/SVL	0.241 ± 0.035	0.174	0.289	0.219 ± 0.051	0.155	0.276	0.265 ± 0.022	0.2[illegible]5	0.312	0.221 ± 0.032	0.165	0.252
F1/SVL	0.146 ± 0.025	0.1[illegible]0	0.188	0.152 ± 0.024	0.[illegible]21	0.[illegible]91	0.[illegible]95 ± 0.0[illegible]2	0.[illegible]51	0.230	0.156 ± 0.0[illegible]7	0.132	0.1[illegible]
F2/SVL	0.1[illegible]1 ± 0.0[illegible]3	0.100	0.150	0.123 ± 0.017	0.093	0.[illegible]48	0.[illegible]54 ± 0.028	0.[illegible]20	0.252	0.142 ± 0.020	0.127	0.[illegible]80
F3/SVL	0.1[illegible] ± 0.0[illegible]8	0.128	0.[illegible]	0.[illegible]87 ± 0.01[illegible]	0.161	0.[illegible]08	0.[illegible]88 ± 0.016	[illegible]	0.27[illegible]	0.18[illegible] ± 0.009	0.170	0.19[illegible]
F4/SVL	0.133 ± 0.015	0.109	0.161	0.127 ± 0.023	0.099	0.[illegible]55	0.[illegible]42 ± 0.027	0.[illegible]14	0.239	0.149 ± 0.0[illegible]3	0.133	0.162
HLL/SVL	1.408 ± 0.051	1.320	1.538	1.423 ± 0.098	[illegible]317	[illegible]589	1.469 ± 0.10[illegible]	1.3[illegible]5	1.773	1.496 ± 0.047	1.423	[illegible]534
FL/SVL	0.439 ± 0.026	0.404	0.497	0.480 ± 0.0[illegible]18	0.457	0.516	0.484 ± 0.0[illegible]30	0.428	0.564	0.467 ± [illegible]	0.4[illegible]	0.5[illegible]9
TL/SVL	0.4[illegible] ± 0.027	[illegible]4[illegible]0	0.5[illegible]9	0.486 ± 0.0[illegible]26	0.450	0.516	0.50[illegible] ± 0.0[illegible]36	0.449	0.600	0.480 ± 0.0[illegible]1	0.46[illegible]	0.494
FOL/SVL	0.487 ± 0.034	[illegible]390	0.5[illegible]3	0.466 ± 0.025	0.425	0.497	0.485 ± 0.0[illegible]40	0.411	0.615	0.499 ± 0.022	0.468	0.5[illegible]2
T1/SVL	0.173 ± 0.023	0.140	0.237	0.168 ± 0.023	0.[illegible]47	0.204	0.181 ± 0.03	0.171	0.258	0.[illegible]97 ± 0.0[illegible]7	0.[illegible]75	0.[illegible]70
T2/SVL	0.246 ± 0.023	0.[illegible]02	0.[illegible]86	0.233 ± 0.015	0.22[illegible]	0.264	0.245 ± 0.034	0.196	0.[illegible]65	0.249 ± 0.0[illegible]7	0.230	[illegible]
T3/SVL	0.3[illegible]9 ± 0.030	[illegible]23	0.367	0.324 ± 0.019	0.308	0.351	0.348 ± 0.0[illegible]3	0.[illegible]73	0.[illegible]98	0.341 ± 0.025	[illegible]	[illegible]
T4/SVL	0.390 ± 0.023	0.336	0.427	0.375 ± 0.0[illegible]	0.348	0.411	0.401 ± 0.043	0.[illegible]	0.479	0.4[illegible]9 ± 0.031	0.384	0.46[illegible]
T5/SVL	0.328 ± 0.026	[illegible]28	0.370	0.322 ± 0.019	0.308	0.35	[illegible]34 ± 0.0[illegible]	0.[illegible]78	0.403	0.[illegible]76 ± 0.021	0.300	[illegible]
HL/HW	0.87[illegible] ± 0.0[illegible]6	[illegible]8	1.[illegible]9	0.849 ± 0.048	0.75[illegible]	[illegible]98	0.92[illegible] ± 0.0[illegible]5	0.841	[illegible]2	[illegible]98 ± 0.088	0.897	[illegible]4
[illegible]	0.925 ± 0.[illegible]70	[illegible]633	[illegible]273	[illegible]124 ± 0.5[illegible]	0.479	2.000	[illegible]957 ± 0.[illegible]56	0.645	[illegible]47	[illegible]878 ± [illegible]46	[illegible]67	[illegible]059
[illegible]	[illegible]3 ± 0.704	[illegible]650	1.686	0.773 ± 0.[illegible]65	0.568	0.971	[illegible]890 ± 0.1[illegible]5	0.656	[illegible]78	[illegible]873 ± [illegible]092	[illegible]733	[illegible]
[illegible]	1.569 ± 0.309	1.145	2.000	1.505 ± 0.279	1.[illegible]58	[illegible]917	[illegible]45 ± 0.490	0.500	[illegible]700	[illegible]465 ± [illegible]362	1.020	2.067
[illegible]	1.60 ± 0.[illegible]59	0.955	[illegible]35	[illegible]466 ± 0.[illegible]77	0.875	[illegible]917	[illegible]515 ± 0.488	0.548	2.[illegible]	[illegible]60 ± [illegible]224	[illegible]2	[illegible]
F1/F2	[illegible]23 ± 0.[illegible]6	[illegible]922	1.5[illegible]	1.240 ± 0.089	1.[illegible]8	[illegible]326	1.395 ± 0.[illegible]	0.[illegible]05	[illegible]70	[illegible]96 ± [illegible]63	[illegible]855	[illegible]
[illegible]	1.175 ± 0.077	[illegible]865	1.[illegible]96	0.98[illegible] ± 0.04[illegible]	[illegible]910	[illegible]053	1.036 ± 0.[illegible]62	0.[illegible]25	[illegible]150	[illegible]34 ± [illegible]078	0.9[illegible]5	[illegible]6
[illegible]	1.109 ± 0.062	[illegible]966	[illegible]209	0.[illegible]5[illegible] ± 0.038	[illegible]885	0.994	1.0[illegible] ± 0.[illegible]67	0.857	[illegible]98	[illegible]76 ± [illegible]08	0.902	1.20



ig. 8 Scatter plot of individual score of canonical discriminant function 1 (CA1) and 2 (CA2) for *E. aloysii*, *E. cyanophlyctis*, and *E. hexadactylus* (A) and that for *E. mudigere*, *E. cyanophlyctis*, and *E. hexadactylus* (B)

nalysis are shown in tab. 2. The standardized discriminant coefficients were large (in bsolute value) in SVL, HLL and HL for function 1 and in SVL, T4, F1 and F2 for function ' In discriminant analysis using ratios relative to SVL (HL/SVL, HW/SVL, etc.), the listribution pattern of individual scores was nearly the same as in the analysis using neasurements. Mann-Whitney *U* tests showed that nine and 13 body ratios differed ignificantly ($P < 0.01$) between *E. aloysii* and *E. hexadactylus* and between *E. aloysii* nd *E. cyanophlyctis*, respectively (tab. 3-4). The head is smaller in *E. aloysii* than in *I. hexadactylus*, differences of both HL/SVL and HW/SVL of the two species being highly ignificant ($P < 0.01$). The eyelid width is larger and the hindlimb length is smaller, both elative to SVL, in *E. aloysii* than in *E. hexadactylus* ($P < 0.01$). *Euphlyctis aloysii* differs ignificantly from *E. cyanophlyctis* ($P < 0.01$), having a smaller head length, smaller eye liameter, tympanum diameter, femur length and tibia length, all relative to SVL. The ratio IL/HW is significantly smaller, and FOL/FEL is significantly larger in *E. aloysii* than in *E. cyanophlyctis.*

Euphlyctis mudigere was also clearly separated from *E. cyanophlyctis* and *E. hexadactylus* y discriminant analysis (fig. 8B, tab. 2). The standardized coefficients of discriminant unctions revealed that HW, T4, T2 and F3 contributed more to function 1 and T4, TIL nd FOL contributed more to function 2 than the other measurements. Only two and ne body ratios were significantly different ($P < 0.01$) between *E. mudigere* and *E. cyanophlyctis* and between *E. mudigere* and *E. hexadactylus*, respectively (tab. 3-4). The ratios 1/SVL and F2/SVL were significantly smaller in *E. mudigere* than in *E. cyanophlyctis* $P < 0.01$), and N-N/SVL was significantly larger in *E. mudigere* than in *E. hexadactylus* $P < 0.01$). Fingers and toes were shorter in *E. mudigere* than in *E. cyanophlyctis* and *E. hexadactylus.*

Discriminant analysis clearly separated *E. mudigere* from *E. aloysii* (fig. 9A, tab. 2). The tandardized coefficients of the discriminant function were large (in absolute value) in N-E, T4, F1 and SVL. Mann-Whitney *U* tests revealed that the ratios HW/SVL, FEL/SVL and TIL/ EL were significantly larger ($P < 0.01$) and FOL/FEL was significantly smaller ($P < 0.01$) in *E. mudigere* than in *E. aloysii* (tab. 3-4).

Table 4. - Results of Mann-Whitney *U* test between body ratios of *E. aloysii* (*alo*), *E. mudigere* (*mud*), *E. cyanophlyctis* (*cya*) and *E. hexadactylus* (*hex*). *U* and *P* values are given. Symbols * and ** indicate the 5 % and 1 % significance levels, respectively.

Ratio	*alo* vs. *mud*		*alo* vs. *cya*		*alo* vs. *hex*		*mud* vs. *cya*		*mud* vs. *hex*		*cya* vs. *hex*	
	U	*P*	*U*	*P*	*U*	*P*	*U*	*P*	*U*	*P*	*U*	*P*
HL/SVL	69	0.478	88	0.001 **	6	0.001 **	52	0.402	7	0.046 *	19	0.016 *
HW/SVL	23	0.004 **	158	0.087	18	0.005 **	37	0.088	20	0.886	32	0.112
S-N/SVL	56	0.186	106	0.003 **	19	0.006 **	62	0.795	20	0.886	37	0.203
N-N/SVL	60	0.257	148	0.050	0	0.000 **	34	0.060	0	0.003 **	23	0.031 *
N-E/SVL	81	0.887	103	0.002 **	4	0.000 **	55	0.506	12	0.199	13	0.005 **
ED/SVL	30	0.011 *	33	0.000 **	37	0.070	66	0.977	11	0.153	20	0.019 *
E-E/SVL	52	0.131	227	0.980	34	0.049 *	53	0.435	4.5	0.018 *	29	0.075
ELW/SVL	79	0.813	173.5	0.183	14	0.003 **	49	0.312	7	0.046 *	27	0.056
TD/SVL	63	0.321	54	0.000 **	60	0.534	39	0.112	19	0.775	19	0.016 *
HAL/SVL	67	0.422	100	0.002 **	46	0.178	30	0.035 *	21	1.000	5	0.001 **
F1/SVL	70	0.508	32	0.000 **	52	0.300	11	0.001 **	19	0.775	8	0.002 **
F2/SVL	73	0.603	37	0.000 **	20	0.007 **	16	0.004 **	7	0.046 *	36	0.181
F3/SVL	52	0.131	113.5	0.004 **	43	0.133	54	0.470	20	0.886	43	0.373
F4/SVL	76	0.705	181	0.250	26	0.017 *	51	0.370	9	0.086	35	0.162
HLL/SVL	80	0.850	139	0.030 *	14	0.003 **	48	0.285	11	0.153	38	0.227
FEL/SVL	9	0.000 **	69.5	0.000 **	39	0.087	55	0.506	14	0.317	44	0.408
TIL/SVL	66	0.395	106	0.003 **	49	0.233	45	0.214	16	0.475	31	0.098
FOL/SVL	50	0.108	197	0.448	56	0.407	53	0.435	7	0.046 *	39	0.252
T1/SVL	73	0.603	193	0.392	31	0.034 *	44	0.193	8	0.063	33	0.127
T2/SVL	62	0.299	224	0.922	55	0.378	45	0.214	9	0.086	43	0.373
T3/SVL	76	0.705	163	0.112	41	0.108	50	0.340	12	0.199	50	0.656
T4/SVL	56	0.186	211	0.678	35	0.055	41	0.140	9	0.086	39	0.252
T5/SVL	70	0.508	177	0.212	70	0.917	45	0.214	18	0.668	40	0.279
HL/HW	60	0.257	115	0.006 **	17	0.004 **	31	0.040 *	5	0.022 *	39	0.252
S-N/N-E	53	0.143	211.5	0.686	63.5	0.659	46	0.236	2	0.199	46.5	0.503
TD/ED	50.5	0.141	218	0.807	67.5	0.815	42	0.157	14	0.317	48.5	0.588
N-N/E-E	72.5	0.587	183.5	0.276	58.5	0.484	61.5	0.773	19	0.775	55.5	0.924
ELW/E-E	72.5	0.587	217	0.788	71.5	0.979	58.5	0.644	17	0.568	54.5	0.874
F1/F2	68.5	0.464	161.5	0.104	50	0.254	51	0.370	11	0.153	24.5	0.039 *
TIL/FEL	19	0.002 **	154.5	0.072	44	0.147	32	0.046 *	10	0.116	53	0.799
FOL/FEL	2	0.000 **	49	0.000 **	60	0.534	34	0.060	6	0.032 *	28	0.065

Finally, all four *Euphlyctis* species from Karnataka were separated by discriminant analysis (fig. 9B; tab. 2). The standardized coefficients of discriminant functions were large (in absolute value) in SVL, HLL, FEL and HW for function 1, in SVL, F1, T4 and F2 for function 2, and in FOL, SVL, T5 and T4 for function 3. Although the plot range of *E. mudigere* slightly overlapped with those of *E. aloysii* and *E. cyanophlyctis* in fig. 9B, *E. mudigere* was clearly separated along the third axis for discriminant function 3, scores for function 3 being from 2.431 to 4.263 for *E. mudigere*, from −2.931 to 1.016 for *E. aloysii* and from −2.629 to 1.374 for *E. cyanophlyctis*.

DISCUSSION

Many lines of evidence suggest the existence of a considerable amount of genetic divergence between populations of the wide-ranging *E. cyanophlyctis* populations. KHAN (1997) described a subspecies of *E. cyanophlyctis* from the northwestern highlands of Pakistan as *E. cyanophlyctis microspinulata*. DUTTA (1997) considered *E. cyanophlyctis seistanica*, described from Iran by NIKOLSKI (1900) as a variety, as a valid subspecies. ALAM et al. (2008) clarified that each of the *E. cyanophlyctis* populations from southwestern India, Bangladesh and Sri Lanka constitutes distinct clusters in the phylogenetic tree constructed on the basis of mtDNA sequence data. Remarkable acoustic differences between southwestern and northeastern populations of Indian *E. cyanophlyctis* (ROY & ELEPFANDT, 1993, KURAMOTO &

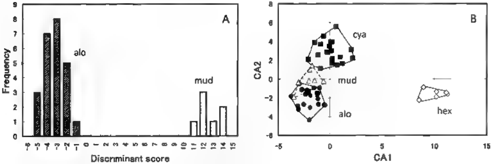


Fig. 9 - Distribution of discriminant scores of *E. aloysii* and *E. mudigere* (A) and scatter plot of individual score of canonical discriminant function 1 (CA1) and 2 (CA2) for *E. aloysii*, *E. mudigere*, *E. cyanophlyctis* and *E. hexadactylus* (B).

JOSHY, in press) may reflect genetic divergence between the two Indian populations. It seems highly probable that future studies will reveal the existence of several cryptic species allied to *E. cyanophlyctis*.

The type locality of *E. cyanophlyctis* (*Rana cyanophlyctis*) is probably Tranquebar (Tarangambadi) in east-central Tamil Nadu, India (BAUER, 1998). Although TIWARI (1991) regarded Kerala, most of Tamil Nadu and southwestern Karnataka as belonging to the Malabar faunal province in the Ceylonese sub-region of the Oriental faunal region, this does not mean the genetic identity of *E. cyanophlyctis* occurs there. Further molecular phylogenetic studies are needed to clarify the relationship of *E. cyanophlyctis* from Karnataka.

The distribution range of *E. hexadactylus* is confined to India, Bangladesh and Sri Lanka. The type locality of this species is south India (FROST, 1985). Although *E. hexadactylus* was reported to have a white or pale yellow venter (DUTTA & MANAMENDRA-ARACHCHI, 1996; CHANDA, 2002; DANIEL, 2002; DANIELS, 2005), all six specimens from Mangalore have a finely mottled pattern on the venter and lower side of the thigh, which is never observed in *E. aloysii*, *E. mudigere* and *E. cyanophlyctis*. The rather heavily mottled underside observed in the *E. hexadactylus* specimens examined in this study indicates genetic differentiation within this species. Thus, the taxonomic situation of *E. hexadactylus* from Karnataka is similar to that of *E. cyanophlyctis* mentioned above.

Euphlyctis ehrenbergii had long been synonymized with *E. cyanophlyctis* and was resurrected by DUBOIS (1981). This species is relatively large in size and has a uniformly greenish dorsum (LEVITON et al., 1992; KHAN, 1997), resembling *E. hexadactylus*. BOULENGER (1920) gave measurements for eight specimens of *E. ehrenbergii* (as *Rana cyanophlyctis* from Saudi Arabia and Yemen), and this species was clearly separated from *E. cyanophlyctis* ($n = 9$) and *E. hexadactylus* ($n = 8$) both from southern India and Sri Lanka by discriminant analysis using his measurements (fig. 10A; tab. 2). Comparisons for body ratios revealed that HL/SVL and F1/F2 of *E. ehrenbergii* were greater ($P < 0.01$) than those of *E. cyanophlyctis* and F1/SVL, F4/SVL, TIL/SVL and TIL/FEL were larger ($P < 0.01$) and F1/F2 was smaller ($P < 0.01$) than those of *E. hexadactylus*. These comparisons give morphometric bases for the specific distinctness of *E. ehrenbergii*.

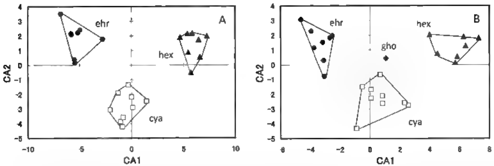


Fig. 10 – Scatter plot of individual score of canonical discriminant function 1 (CA1) and 2 (CA2) for *E. cyanophlyctis*, *E. hexadactylus*, both from south India and Sri Lanka, and *E. ehrenbergii* from Saudi Arabia and Yemen (A). On the scatter plot for the above three species (based on lower number of variables), the score of *E. ghoshi* calculated from the coefficients for the three species is plotted (B). Data from Boulenger (1920) and Chanda (1990).

Roy & Elepfandt (1993) revealed acoustic differences between *E. ehrenbergii* and *E. cyanophlyctis*. Acoustic features of *E. hexadactylus* were analyzed by Kuramoto & Joshy (in press), which seemed rather similar to *E. ehrenbergii* than to *E. cyanophlyctis*. The *E. hexadactylus* population from Bangladesh was proved to belong to a new undescribed taxon by molecular evidence (Alam et al., 2008).

Chanda (1990), in describing *E. ghoshi* (as *Rana ghoshi*), suggested the close relationships of *E. ghoshi* with *E. cyanophlyctis* (as *Rana cyanophlyctis*), *Lankanectes corrugatus* (Peters, 1863) (as *Rana corrugata*) and *Chrysopaa sternosignata* (Murray, 1885) (as *Rana sternosignata*). Each of these genera belongs in a different tribe in the subfamily Dicroglossinae or different subfamily in the Ranidae (Dubois, 2005), and the phylogenetic relationship of *E. ghoshi* must wait for future studies. Chanda (1990) gave measurements for the holotype of *E. ghoshi*. When the discriminant scores for this *E. ghoshi* specimen were calculated using the coefficients of canonical discriminant functions for *E. ehrenbergii*, *E. cyanophlyctis* and *E. hexadactylus* (all data from Boulenger, 1920, as in fig. 10A, except F4, TIL, FOL and T5 which were lacking for *E. ghoshi*, and forelimb length which was measured apparently in different ways by Boulenger, 1920 and by Chanda, 1990), the plot was separated from the ranges of the other three species (fig. 10B, tab. 2). In view of the fact that the ratios snout-length/SVL (15.0), ED/SVL (13.3), and E-E/SVL (6.7) of *E. ghoshi* were larger and HLL/SVL (126.7), T3/SVL (24.2) and TD/ED (0.5) were smaller than the maximum and minimum values, respectively, for *E. ehrenbergii*, *E. cyanophlyctis* and *E. hexadactylus*, *E. ghoshi* seemed to be related rather remotely with the other three *Euphlyctis* species. The snout of *E. ghoshi* (fig. 1 in Chanda, 1990) was round which is unlike the rather pointed snouts of congeners.

The genus *Euphlyctis* has many taxonomic problems to be solved as mentioned above, and future studies may reveal several new cryptic species, as in "*Fejervarya limnocharis*", which was once considered to have an extensive distribution range and recently was split into many species (Dubois & Ohler, 2000; Fei et al., 2002, Kuramoto et al., 2007, Matsui et al., 2007).

ACKNOWLEDGEMENTS

We thank Rev Fr Swebert D'Silva, the Principal of St Aloysius College, and Rev Fr Leo D'Souza for support and facilities to carry out the research, and J. D'Souza and K. G. Yogish for aid in the field SHJ thanks Jesuit Educational Society for the support, and Melwyn Sequeira and Santhosh Wilson for aid in the laboratory

LITERATURE CITED

ALAM, M. S., IGAWA, T., KHAN, M. M. R., ISLAM, M. M., KURAMOTO, M., MATSUI, M., KURABAYASHI, A. & SUMIDA, M., 2008. Genetic divergences and evolutionary relationships in six species of genera *Hoplobatrachus* and *Euphlyctis* (Amphibia Anura) from Bangladesh and other Asian countries revealed by mitochondrial gene sequences. *Molec. Phylogenet. Evol.*, **48** 515-527

BAUER, A. M., 1998. South Asian herpetological specimens of historical note in the Zoological Museum, Berlin. *Hamadryad*, **23** (2): 133-149

BIJU, S. D., 2001. A synopsis of the frog fauna of the Western Ghats, India. *Occ. Publ. ISCB*, **1** 1-24.

BIJU, S. D. & BOSSUYT, F., 2003. New frog family from India reveals an ancient biogeographical link with the Seychelles. *Nature*, **425**, 711-714

----- 2005. Two new *Philautus* (Anura Rhacophoridae Rhacophorinae) from Ponmudi Hill in the Western Ghats of India. *Copeia*, **2005** (1). 29-37

----- 2006. – Two new species of *Philautus* (Anura, Ranidae, Rhacophorinae) from the Western Ghats, India. *Amphibia-Reptilia*, **27** (1) 1-9

BIJU, S. D., VAN BOCXLAER, I., GIRI, V. B., ROELANTS, K., NAGARAJU, J. & BOSSUYT, F., 2007. A new night frog *Nyctibatrachus minimus* sp. nov. (Anura Nyctibatrachidae) the smallest frog from India. *Curr. Sci.*, **93** (6): 854-858

BOULENGER, G. A., 1890. *The fauna of British India, including Ceylon and Burma. Reptilia and Batrachia* London, Taylor and Francis. i-xvii + 1-541

----- 1920. A monograph of South Asian, Papuan, Melanesian and Australian frogs of the genus *Rana*. *Rec. ind. Mus.*, **20**: 1-226

CASTRESANA, J., 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molec. Biol. Evol.*, **17**: 540-552

CHANDA, S. K., 1990. A new frog of the genus *Rana* (Ranidae Anura) from Manipur, northeastern India. *Hamadryad*, **15** (1). 16-17.

----- 2002. – *Hand book – Indian amphibians*. Kolkata, ZSI: i-vii + 1-335

DANIEL, J. C., 2002. *The book of Indian reptiles and amphibians*. Oxford, Oxford Univ. Press. i-viii + 1-238

DANIELS, R. J. R., 2005. *Amphibians of peninsular India*. Hyderabad, Universities Press (India) Private Ltd.: i-xii + 1-268, 56 pl

DUBOIS, A., 1981. Liste des genres et sous-genres nominaux de Ranoidea (Amphibiens Anoures) du monde, avec identification de leurs especes-types: consequences nomenclaturales. *Monit. zool. ital.* (n.s.), **15** (suppl.): 225-284

----- 1992. Notes sur la classification des Ranidae (Amphibiens Anoures). *Bull. mens. Soc. linn. Lyon*, **61** (10). 305-352

----- 2005. *Amphibia Mundi* 1.1. An ergotaxonomy of recent amphibians. *Alytes*, **23** (1-2) 1-24

DUBOIS, A. & OHLER, A., 2000. Systematics of *Fejervarya limnocharis* (Gravenhorst, 1829) (Amphibia, Anura, Ranidae) and related species. 1. Nomenclatural status and type-specimens of the nominal species *Rana limnocharis* Gravenhorst, 1829. *Alytes*, **18**(1-2): 15-50

----- 2001. A new genus for an aquatic ranid (Amphibia, Anura) from Sri Lanka. *Alytes*, **19** (2-4) 81-106

DUBOIS, A., OHLER, A. & BIJU, S. D., 2001. A new genus and species of Ranidae (Amphibia, Anura) from south-western India. *Alytes*, **19** (2-4) 53-79

Dutta, S. K., 1997. – *Amphibians of India and Sri Lanka (Checklist and bibliography)*. Bhubaneshwar, Odyssay Publishing House: i-xiii + 1-342.

Dutta, S. K. & Manamendra-Arachchi, K., 1996. – *The amphibian fauna of Sri Lanka*. Colombo, Wildlife Heritage Trust of Sri Lanka: 1-230.

Farris, J. S., Kallersiö, M., Kluge, A. G. & Bult, C., 1995. – Testing significance of incongruence. *Cladistics*, **10**: 537-553.

Fei, L., Ye, C.-Y., Jiang, J.-P. & Xie, F., 2002. – On taxonomic status of *Rana limnocharis* group with revision of nomenclature of the rice frog from China. *Herp. sin.*, **9**: 88-96. [In Chinese]

Fouquet, A., Vences, M., Salducci, M. D., Meyer, A., Marty, C., Blanc, M. & Gilles, A., 2007. – Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax rubber* and *Rhinella margaritifera* species groups. *Molec. Phylogenet. Evol.*, **43**: 567-582.

Frost, D. R. (ed.), 1985. – *Amphibian species of the world*. Lawrence, Allen Press & Ass. Syst. Coll.: [i-iv] + i-v + 1-732.

Khan, M. S., 1997. – A new subspecies of common skittering frog *Euphlyctis cyanophlyctis* (Schneider, 1799) from Balochistan, Pakistan. *Pakistan J. Zool.*, **29** (2): 107-112.

Kurabayashi, A., Kuramoto, M., Joshy, H. & Sumida, M., 2005. – Molecular phylogeny of the ranid frogs from southwest India based on the mitochondrial ribosomal RNA gene sequences. *Zool. Sci.*, **22**: 525-534.

Kuramoto, M. & Joshy, S. H., 2003. – Two new species of the genus *Philautus* (Anura: Rhacophoridae) from the Western Ghats, southwestern India. *Curr. Herp.*, **22** (2): 51-60.

----- 2006. – Morphological and acoustic comparisons of *Microhyla ornata*, *M. fissipes*, and *M. okinavensis* (Anura: Microhylidae). *Curr. Herp.*, **25** (1): 15-27.

----- in press. – Advertisement call of Indian and Sri Lankan frogs. *J. Bombay nat. Hist. Soc.*

Kuramoto, M., Joshy, S. H., Kurabayashi, A. & Sumida, M., 2007. – The genus *Fejervarya* (Anura: Ranidae) in central Western Ghats, India, with descriptions of four new cryptic species. *Curr. Herp.*, **26** (2): 81-105.

Leviton, A. E., Anderson, S. C., Adler, K. & Minton, S. A., 1992. – *Handbook to Middle East amphibians and reptiles*. Oxford, Ohio, Soc. Stud. Amph. Rept.: i-vii + 1-252.

Liu, Z. Q., Wang, Y. Q. & Su, B., 2005. – The mitochondrial genome organization of the rice frog, *Fejervarya limnocharis* (Amphibia: Anura): a new gene order in the vertebrate mtDNA. *Gene*, **346**: 145-151.

Matsui, M., Toda, M. & Ota, H., 2007. – A new species of frog allied to *Fejervarya limnocharis* from the southern Ryukyus, Japan (Amphibia: Ranidae). *Curr. Herp.*, **26** (2): 65-79.

Nikolski, A. M., 1900. – Reptiles, amphibians and fishes collected on the voyage of Mr. N. A. Zaroundny to Persia in 1898. *Annuaire Mus. St. Petersb.*, **4**: 406. [In Russian, not seen, quoted after Dutta, 1997]

Posada, D. & Crandall, K. A., 1998. – Modeltest: testing the model of DNA substitution. *Bioinformatics*, **14**: 817-818.

Ronquist, F. & Huelsenbeck, J. P., 2003. – MrBayes 3; Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**: 1572-1574.

Roy, D. & Elepfandt, A., 1993. – Bioacoustic analysis of frog calls from northeast India. *J. Biosci.*, **18** (3): 383-393.

Swofford, D. L., 2001. – *PAUP* Phylogenetic analysis using parsimony (* and other methods), version 4*. Sunderland, MA, Sinauer.

Tiwari, S. K., 1991. – *Zoogeography of Indian amphibians*. New Delhi, Today & Tomorrow's Printers and Publishers: i-iv + 1-187.

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G., 1997. – The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acid Res.*, **24**: 4876-4882.

Vences, M., Thomas, M., Van Der Meijen, A., Chiari, Y. & Vieites, D. R., 2005. – Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. *Front. Zool.*, **2**: 5.

Alytes, 2009, **26** (1-4): 117-152.

Terminal phalanges in ranoid frogs: morphological diversity and evolutionary correlation with climbing habits

Marjolein Kamermans* & Miguel Vences**

* School of Natural Sciences, Trinity College, University of Dublin, Dublin 2, Ireland

** Division of Evolutionary Biology, Zoological Institute,
Technical University of Braunschweig,
Spielmannstr. 8, 38106 Braunschweig, Germany
Corresponding author: <m.vences@tu-bs.de>

We provide a descriptive survey of the morphological diversity of the shape of terminal phalanges of fingers and toes in ranoid frogs, based on analysis of 124 species of 64 genera, belonging to the Arthroleptidae (including Arthroleptinae, Astylosterninae and Leptopelinae), Brevicipitidae, Ceratobatrachidae, Dicroglossidae, Hemisotidae, Hyperoliidae, Mantellidae, Microhylidae, Petropedetidae, Phrynobatrachidae, Ptychadenidae, Pyxicephalidae, Ranidae and Rhacophoridae. For comparative purposes, specimens of 26 species of 18 genera belonging to ten non-ranoid frog families were also surveyed. The bones were analysed macroscopically as well as using scanning electron microscopy. Terminal phalanges were classified into 13 character states, called A to M, and into three major character state groups: (I) pointed tips, (II) rounded and relatively broad tips, (III) bifurcated tips. Eight character states were observed within ranoids, and six of these also occurred in non-ranoid taxa; five further states were found exclusively in the non-ranoid taxa. In order to assess homoplasy and possible adaptive significance for this osteological character, we compiled, from recent molecular studies, a consensus tree of the ranoid genera studied here. Tracing the evolution of all character states along this phylogeny was largely ambiguous but became more feasible when summarizing character states of distally enlarged (bifurcated or mushroom-shaped) vs. non-enlarged phalanges. Non-enlarged phalanges were supported as ancestral states in most clades, and an independent evolution towards distally enlarged phalanges was indicated in 12 clades, plus two reversals and two ambiguous transformations. Concentrated-changes tests supported a significant association of the evolution of distally enlarged phalanges with climbing habits, indicating an important adaptive component that likely explains the high degree of homoplasy in this skeletal character.

INTRODUCTION

At deep phylogenetic levels, amphibians show a high degree of morphological homoplasy (e.g., Mueller et al., 2004; Van der Meijden et al., 2005). Especially frogs are characterized by a highly derived *bauplan* that possibly allows only a limited number of general variations in order to adapt to certain ecological niches (EMERSON, 1986). For instance, arboreal frogs in families that belong to different major clades can be extremely similar externally, characterized by a broad head with large eyes, enlarged terminal pads on fingers and toes, and often also other characters such as extended webbing between toes and sometimes fingers, a smooth dorsal skin without longitudinal folds, or the lack of a sharp border between dorsal and lateral colour. Neotropical species of the Hylidae can be so similar to Asian species of the unrelated Rhacophoridae that a familial diagnosis is merely impossible without examining osteological features such as shoulder girdle structure or the form of the terminal phalanx bones of fingers and toes. Sand frogs (the genus *Tomopterna* in the family Ranidae) were long believed to contain African as well as Asian and one Madagascan species based on their external similarity, but molecular work (BOSSUYT & MILINKOVITCH, 2000; VENCES & GLAW, 2001) demonstrated that the three geographic assemblages belong to different and not closely related clades, namely the African *Tomopterna* to the Pyxicephalidae, the Asian species (as genus *Sphaerotheca*) to the Dicroglossidae, and the Madagascan species (as *Laliostoma labrosum*) to the Mantellidae. Among African frogs, recent molecular work (VAN DER MEIJDEN et al., 2005; FROST et al., 2006) highlighted an endemic clade, the Pyxicephalidae, that in addition to *Tomopterna* contains a variety of other anuran genera of such diversity that before they had been classified into five different subfamilies.

Whereas general external morphology of frogs is certainly subjected to strong homoplasy, osteological feautures are usually attributed important value for reconstructing anuran phylogeny. In fact, several character states such as a firmisternal shoulder girdle are well suited to define certain derived clades of frogs, for example the Ranoidea. However, many of these states have evolved convergently in other clades of the amphibian tree, e.g., the firmisternal shoulder girdle in dendrobatids, atelopodine bufonids and pipids. Similar to external characters, several features of shoulder girdle morphology are probably under selective pressure as they may be relevant for locomotion, such as the shape of the omosternum (forked or unforked), the ratio of omosternum/sternal style length, or the general arciferal or firmisternal state (EMERSON, 1983). The same may apply to most other osteological features of anurans, but detailed analyses of functional morphology of these elements are surprisingly rare.

A further example for homoplasy in frog osteology is found in the presence of an intercalary element between the terminal and the penultimate phalanx of fingers and toes, a character first described by LEYDIG (1876) in *Hyla arborea*. It has been considered of great phylogenetic value to define Old World tree frogs (e.g., LIEM, 1970), but it is now clear that this element evolved convergently in at least the Hyperoliidae, Arthroleptidae (genus *Leptopelis*), Rhacophoridae/Mantellidae, Microhylidae (genus *Phrynomantis*), Centrolenidae and Hylidae, and possibly reversed in one mantellid clade (genus *Laliostoma*).

Nevertheless, early studies of anuran systematics and phylogeny were largely based on osteological features (e.g., NOBLE, 1931; PARKER, 1934, LAURENT, 1940, 1941*a-b*, 1943*a-b*, 1944). In ranoid frogs, LIEM (1970) studied the phylogeny of Old World treefrogs based on 36 characters, 14 of which were osteological characters of the skull, vertebrae, pectoral girdle, hyoid skeleton, carpals, tarsals, metacarpals and terminal phalanges. CLARKE (1981) examined 22 osteological characters of the skull, pectoral girdle, vertebrae, ilium and the terminal phalanges in African ranids; and DREWES (1984) studied 30 morphological characters of which 21 osteological characters of the skull, pectoral girdle, hyoid apparatus, carpals, tarsals and terminal phalanges. CHANNING (1989) combined and re-analyzed the data of LIEM (1970) and DREWES (1984). More recently, SCOTT (2005) studied 178 morphological characters, 101 of which were osteological. Several other studies have focused on particular osteological characters and analyzed their variation in specific groups of ranoid frogs, or across frogs in general, including ranoids (e.g., LAURENT & FABREZI, 1985, 1990; FABREZI & ALBERCH, 1996, FABREZI & EMERSON, 2003; MANZANO et al., 2007).

One of the characters used in all these studies is the shape of the terminal phalanx bones of fingers and toes (see also DECKERT, 1938; TIHEN, 1965; PERRET, 1966; LYNCH, 1971; HEYER, 1975). However, the numbers and definitions of states described for this character were different, with LIEM (1970) and DREWES (1984) recognizing four states, CLARKE (1981) recognizing seven states, and SCOTT (2005) recognizing three states in the fingers and seven states in the toes. Variability in the phalanx shape within individuals has been noted (HEYER, 1975; CLARKE, 1981), an adaptive value of this character postulated (DREWES, 1984), and problems in a clear categorization in character states emphasized (CLARKE, 1981) FABREZI (1996) undertook a wide survey of these characters in various neobatrachian frog lineages and observed a high degree of homoplasy in these bones, both regarding shape and development.

In this paper, we undertake a wide survey of the morphology of terminal phalanx shape in frogs, mainly focusing on ranoid frogs. This group corresponds to the superfamily Ranoidea as understood by DUBOIS (1992, 2005), with a taxonomic content similar to the unranked taxon "Ranoides" created and defined by FROST et al. (2006).

Based on examination of cleared and stained specimens and scanning electron microscopic pictures, we provide detailed descriptions of the variation observed in this state. We further analyse the evolution of this character along an informal supertree of these frogs based on recent molecular studies, and use comparative methods to test for the influence of the general ecological habits on this skeletal character

MATERIAL AND METHODS

This study is based on an analysis of 124 species of 64 genera, belonging to the following ranoid families as recognized by FROST et al (2006). Arthroleptidae (including Arthroleptinae, Astylosterninae and Leptopelinae), Brevicipitidae, Ceratobatrachidae, Dicroglossidae, Hemisotidae, Hyperoliidae, Mantellidae, Microhylidae, Petropedetidae, Phrynobatrachidae, Ptychadenidae, Pyxicephalidae, Ranidae and Rhacophoridae For comparative purposes, also specimens of 26 species of 20 genera belonging to ten non-ranoid frog families were surveyed. Altogether, we screened cleared and stained skeletons of 190 ranoid and 29 non-ranoid specimens. The appendix provides a list of all specimens that were examined, with the collections where they are deposited

The family-level classification used herein follows almost fully the recent proposal by FROST et al. (2006). This work certainly constitutes a great progress in anuran systematics, especially because an overdue partitioning of several large, heterogeneous and partly not monophyletic families has been undertaken by these authors. On the other hand, several of the new arrangements, such as sinking the Leptopelinae and Astylosternidae in the family Arthroleptidae, or the Nasikabatrachidae into the Sooglossidae, may have been premature and recognition and revalidation of a few additional families will probably be a theme in future studies of anuran systematics. However, since such proposals are far beyond the scope of the present paper, we here follow the family-level taxonomy proposed by FROST et al. (2006), with a few exceptions only (we recognize the Astylosterninae as a subfamily of the Arthroleptidae, and continue using the genus name *Phrynodon*, to make it easier to refer to these frogs in the text), and we continue accepting Laliostominae as a mantellid subfamily (see GLAW & VENCES, 2006, GLAW et al., 2006). Species belonging to the following genera have been studied: *Afrixalus* Laurent, 1944; *Agalychnis* Cope, 1864; *Aglyptodactylus* Boulenger, 1919, *Ameerega* Bauer, 1986, *Anodonthyla* Müller, 1892, *Arthroleptis* Smith, 1849; *Astylosternus* Werner, 1898; *Batrachylodes* Boulenger, 1887; *Blommersia* Dubois, 1992; *Bombina* Oken, 1816, *Boophis* Tschudi, 1838, *Breviceps* Merrem, 1820, *Cacosternum* Boulenger, 1887; *Callulella* Stoliczka, 1872; *Ceratobatrachus* Boulenger, 1884; *Chiromantis* Peters, 1854; *Colostethus* Cope, 1866, *Cophixalus* Boettger, 1892, *Cophyla* Boettger, 1880; *Dendrobates* Wagler, 1830; *Dermatonotus* Méhely, 1904; *Discoglossus* Otth, 1837; *Epipedobates* Myers, 1987, *Euphlyctis* Fitzinger, 1843; *Fejervarya* Bolkay, 1915; *Gastrophryne* Fitzinger, 1843; *Gephyromantis* Methuen, 1920; *Guibemantis* Dubois, 1992; *Heleophryne* Sclater, 1898; *Hemisus* Günther, 1859; *Heterixalus* Laurent, 1944, *Hoplobatrachus* Peters, 1863; *Hyalinobatrachium* Ruiz-Carranza & Lynch, 1991; *Hyla* Laurenti, 1768; *Hylarana* Tschudi, 1838; *Hymenochirus* Boulenger, 1896; *Hyperolius* Rapp, 1842, *Kaloula* Gray, 1831, *Kassina* Girard, 1853; *Kurixalus* Ye, Fei & Dubois, 1999; *Laliostoma* Glaw, Vences & Bohme, 1998, *Leptodactylodon* Andersson, 1903, *Leptopelis* Günther, 1859, *Limnodynastes* Fitzinger, 1843, *Limnonectes* Fitzinger, 1843; *Lithobates* Fitzinger, 1843; *Mantella* Boulenger, 1882; *Mantidactylus* Boulenger, 1895; *Megophrys* Kuhl & Van Hasselt, 1822, *Microhyla* Tschudi, 1838, *Nanorana* Günther, 1896, *Natalobatrachus* Hewitt & Methuen, 1912; *Occidozyga* Kuhl & Van Hasselt, 1822, *Odorrana* Fei, Ye & Huang, 1990; *Oophaga* Bauer, 1994, *Petropedetes* Reichenow, 1874, *Phlyctimantis* Laurent & Combaz, 1950, *Phrynobatrachus* Günther, 1862; *Phrynodon* Parker, 1935; *Phrynomantis* Peters, 1867, *Pipa* Laurenti, 1768; *Platymantis* Gunther, 1859, *Polypedates* Tschudi, 1838, *Pseudophryne* Fitzinger, 1843, *Ptychadena* Boulenger, 1917, *Quasipaa* Dubois, 1992; *Rana* Linnaeus, 1758, *Rhacophorus* Kuhl & Van Hasselt, 1822, *Rhinoderma* Duméril & Bibron, 1841, *Scaphiophryne* Boulenger, 1882; *Scotobleps* Boulenger, 1900; *Silurana* Gray, 1864; *Sphaerotheca* Günther, 1859, *Spinomantis* Dubois, 1992, *Staurois* Cope, 1865; *Strongylopus* Tschudi, 1838; *Tachycnemis* Fitzinger, 1843, *Tomopterna* Duméril & Bibron, 1841; *Trichobatrachus* Boulenger, 1900, *Xenopus* Wagler, 1827

Clearing and staining was carried out according to standard protocols (DINGERKUS & UHLER, 1977) as modified by PLÖSCH (1991). The third finger and the fourth toe are generally the longest digits, and terminal phalanx morphology is usually best expressed in these digits, although terminal finger phalanx morphology does not necessarily correspond with that of the toes (CLARKE, 1981) Except for a few specimens where the hand bones were disconnected and a precise identification was not possible, the present study is focused on a comparison of the terminal phalanx of the third digit of the hand This bone was drawn under a stereo microscope equipped with a camera lucida, mostly from the dorsal side The drawings were used to attain a preliminary categorisation of character states On this basis, we selected representative specimens for each state for closer examination by scanning electron microscopy (SEM). Further SEM analyses were carried out on specimens where the character states could not be reliably scored otherwise.

The terminal and the penultimate phalanges of the third finger were removed from the cleared and stained specimens. Tissue remains were then dissolved in KOH, the bones prepared for SEM analysis using standard gold-coating procedures, and studied using a JEOL 35C microscope. The species and specimens for which the terminal phalanx of the third finger (unless mentioned otherwise) has been SEM-pictured are indicated in the appendix and most SEM pictures are reproduced in fig. 1-8. In the following species, other terminal phalanges were SEM pictured. *Fejervarya cancrivora* (also fourth toe), *Gastrophryne* cf. *olivacea* (only fourth toe), *Kassina decorata* (also fourth toe), *Phrynobatrachus mababiensis* (fourth toe), *Phrynobatrachus werneri* (only fourth toe), *Phrynodon* cf *sandersoni* (several terminal phalanges, also first and second finger), *Pipa carvalhoi* (third toe), *Pseudophryne bibronii* (bones disconnected, differentiation between fingers and toes impossible), *Ptychadena mascareniensis* (also fourth toe, ZFMK 55157), *Scaphiophryne brevis* (only fourth finger as the other fingers were missing), *Strongylopus grayii* (only first finger, as the other fingers were disconnected), *Trichobatrachus robustus* (two specimens; the biggest specimen had an extra hook on top of its phalanx which has been pictured as well) and *Xenopus victorianus* (also third toe and fifth finger)

To test for a correlation among climbing habits and shape of terminal phalanges, we transformed these into binary characters (climbing vs. non-climbing, and distally bifurcated vs. non-bifurcated) and traced ancestral character states using both *Acctran* and *Deltran* models in MacClade (MADDISON & MADDISON, 1998). We used the concentrated-changes test of MADDISON (1990) to test the association of changes in these two binary characters (see LORCH & EADIE, 1999) This test determines the probability that various numbers of gains and losses of the dependent variable (terminal phalanx morphology) would occur in certain distinguished areas of the clade selected (defined by climbing habits), given that a certain number of gains and losses occur in the whole clade, and given the null model that changes are randomly distributed among the branches of the clade.

RESULTS

Based on this study, we distinguish a total of 13 character states for the shape of the terminal phalanx of the third finger, named A to M and classified into three major character state groups: (I) pointed tips, (II) rounded and relatively broad tips, (III) bifurcated tips. An additional state, the hook-shaped morphology, was only observed on the terminal phalanges of the toes and it is therefore not coded. Considerable variation was found within species of the same genus, e.g. in *Scaphiophryne* (*S. brevis*, state E, *S. calcarata*, state F, and *S. marmorata*, state H). In some cases, a limited amount of variation was also observed between individuals of the same species. Descriptions of character states given in the following refer largely to the dorsal view, with more complete descriptions from different angles for those species for which SEM pictures were made. For each character state we list the taxa that fit that description, with all deviations from the typical state described in more detail. In species where phalanx morphology of all or some toes was very different from that of the third finger, we give short descriptions also of the deviant toe phalanx morphology.

CHARACTER STATES

State A

From the basis, the terminal phalanx becomes less broad towards the (rounded) tip, which does not end in a bulb. Sometimes the tip is somewhat pentagonal or tetragonal. Observed in: *Afrixalus delicatus*, *A. fornasini*, *A. fulvovittatus* and *A.* sp. (fig. 1a); *Fejervarya cancrivora* (fig. 1c1-d3) and *F. limnocharis*; *Heterixalus alboguttatus*, *H. andrakata*, *H. betsileo*, *H. luteostriatus*, *H. madagascariensis*, *H. punctatus*, *H. rutenbergi*, *H. tricolor* and *H. variabilis*; *Hyperolius argus*, *H. marmoratus*, *H. nasutus*, *H. pusillus*, *H. semidiscus*, *H.* sp. and *H. tuberilinguis*; *Leptodactylodon mertensi*; *Leptopelis bocagii*, *L.* cf. *mossambicus*, *L. modestus*, *L. natalensis* and *L. rufus*; *Megophrys nasuta*, *Occidozyga lima*, *Phyllomedusa sauvagii*.

The terminal phalanx of the *Afrixalus* species studied ends in a pentagonal tip. In both *Fejervarya* species the terminal phalanx of the toe is relatively long. The tip of the terminal toe phalanx is bent towards the ventral side, ending in a small bulb that cannot be recognized from the dorsal side. A bulb at the terminal tip is also present at the fingers, seen from the dorsal side. This small bulb indicates that *Fejervarya* could also fit state F. Seen laterally, the dorsal side of the terminal phalanx is straight, and the ventral side makes an S-curve from the basis towards the tip (fig. 1c1-d3). This S-curve is absent in other genera categorized in state A, although it is typically found in species with a hook-shaped morphology. *Hyperolius* and *Heterixalus* share the same terminal phalanx morphology. In *Leptodactylodon mertensi*, the terminal phalanges of toes and fingers are similar. In *Occidozyga lima*, the tip of the terminal phalanges is somewhat pentagonal as in *Afrixalus*.

State B

This form has only been observed in *Pipa carvalhoi*. The terminal phalanx tip is rounded and not stretched laterally, although it has a protuberance sticking out on top. All fingers are of identical morphology. The toes are similar to state E as described below: the terminal phalanx tip is not perfectly round but a little bumpy.

State C

This form has only been observed in *Xenopus victorianus* (fig. 1e). The terminal phalanx tips of the fingers are split in three. The terminal phalanges of the fourth and fifth toe have two tips without a distinct ridge in between, as if the terminal phalanx tip had been excavated. The terminal phalanges of the first, second and third toe bend towards the ventral side and end in a sharp point, with a tendency towards a hook-shaped morphology.

State D

The phalanx tip is a highly reduced form, found in *Limnodynastes* sp. only. Since no SEM picture was made, further comparisons are not possible.

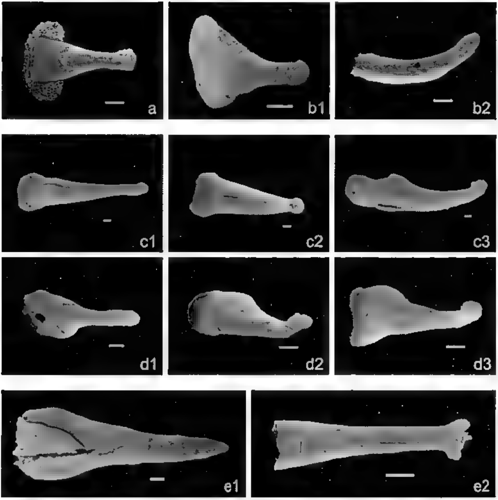


Fig. 1. Scanning electron microscope pictures of terminal phalanges of third finger (unless otherwise mentioned), categorized in morphological states A, A/F and C. (a) *Afrixalus* sp., ventral view, state A, (b1-2) *Leptopelis natalensis*, dorsal and lateral views, state A, (c1-3) *Fejervarya cancrivora*, dorsal, ventral and lateral views, state A/F, (d1-3) *Fejervarya cancrivora*, fourth toe, dorsal, lateroventral and lateral view, state A/F, (e1) *Xenopus victorianus*, fourth toe, dorsal view, state C, (e2) *Xenopus victorianus*, dorsal view, state C. The scale bars represent 100 µm

State E

The tip of the terminal phalanges has no conspicuous shape. It is rounded and slightly cone-shaped, lacking a clearly defined knob or bulb at the end.

The following species are categorized in this state: *Aglyptodactylus madagascariensis* (fig. 2e), *Breviceps fuscus* and *B. mossambicus* (fig. 2a), *Discoglossus galganoi*, *Hemisus*

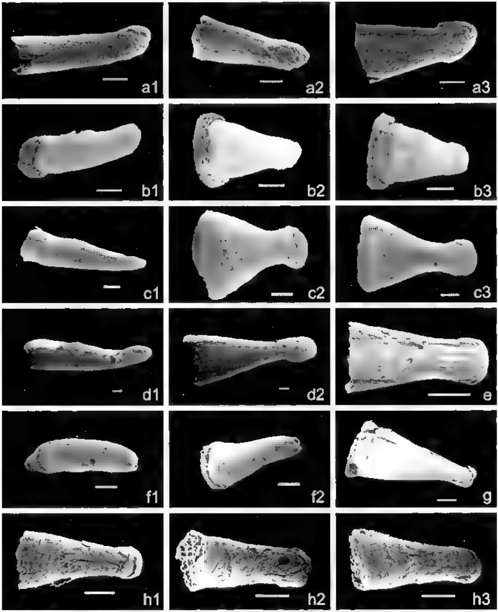


Fig. 2. – Scanning electron microscope pictures of terminal phalanges of third finger, all categorized in morphological state E. (a1-3) *Breviceps mossambicus*, lateral, lateroventral and dorsal views. (b1-3) *Scaphiophryne brevis*, lateral, dorsal and ventral views. (c1-3) *Laliostoma labrosum* (ZFMK 59967), lateral, ventral and dorsal views. (d1-2) *Laliostoma labrosum* (ZFMK 8890), lateral and dorsal views. (e) *Aglyptodactylus madagascariensis*, dorsal view. (f1-2) *Ptychadena mascareniensis*, lateral and dorsal views. (g) *Platymantis corrugatus*, dorsal view. (h1-3) *Pseudophryne bibronii*, finger number unknown, dorsal and ventral views, and dorsal view of another finger of the same individual. The scale bars represent 100 µm.

marmoratus, *Hoplobatrachus chinensis*; *Hyla arborea* and *H. cinerea*; *Laliostoma labrosum* (fig. 2c and 2d), *Platymantis corrugatus* (fig. 2g), *Pseudophryne bibronii*; *Ptychadena* cf. *mascareniensis*, *P. mascareniensis* (fig. 2f), *P. bibroni* (fig. 2h); *Scaphiophryne brevis* (fig. 2b).

In *Aglyptodactylus*, the phalanx tip has a very vague bump at the terminal tip. It is almost a straight line from basis to the tip of the terminal phalanx, only very slightly curved where the bulb/knob would start in state F. *Breviceps* are only tentatively categorized in this state since they show the most reduced form of terminal phalanges of all the species examined. In *Discoglossus galganoi*, the toe phalanges are longer than those of the fingers, but both have an equally rounded tip. In *Hemisus marmoratus*, the toes and fingers have the same shape of terminal phalanges. The two available specimens differ slightly in form. One has phalanx tips that are not shaped in any particular form, rounded and a bit cone-like, without knob form at the end. The tips of the terminal phalanges of the second specimen are also cone-like, but with a highly reduced knob at the end, hence fitting better in state E than in state F. In *Laliostoma*, terminal phalanges are distally with a slight constriction, creating a slight bulb at the tip, which is not obvious enough to place the species in state F. In *Platymantis corrugatus*, from the basis of the terminal phalanx towards the tip, the phalanx becomes narrower. It is most narrow at the point where in state F a constriction would be present. Except for *P. schillukorum*, which is categorized within state F, all *Ptychadena* species studied are categorized within state E, tending towards the morphology of state F. The terminal phalanges tips of the toes of *Ptychadena bibroni* have a hook-shaped morphology. In one of the specimen of *Ptychadena mascareniensis*, the tip does not end in a sharp hook but more pointed.

State F

The distal end of the terminal phalanges is cone-like, generally relatively broad, with a "knob" of various sizes at the end, in some cases with a constriction separating the knob from the remaining phalanx. The following species are categorized in this state: *Astylosternus montanus*, *Bombina* sp.; *Cacosternum boettgeri* (fig. 3c); *Calluella guttulata*; *Ceratobatrachus guentheri* (fig. 3b), *Dermatonotus muelleri*, *Euphlyctis ehrenbergii*, *Fejervarya limnocharis* and *F. cancrivora*; *Limnonectes kuhlii*; *Lithobates catesbeianus*; *Microhyla pulchra*; *Nanorana pleskei*; *Occidozyga martensii*, *Ptychadena schillukorum*, *Quasipaa spinosa*; *Scaphiophryne calcarata* (fig. 3a), *Scotobleps gabonicus*; *Sphaerotheca breviceps*, *Tomopterna delalandii* and *T. natalensis*; *Trichobatrachus robustus*.

In *Astylosternus*, the terminal phalanx of the third finger is not as broad as in most other genera placed within state F and ends in a relatively small knob. The terminal phalanges of the second, third, fourth and fifth toes have a hook-shaped morphology. In *Bombina*, the basis of the terminal phalanx is relatively broad, with a knob as broad as half the size of the basis. In *Cacosternum*, the phalanx is relatively narrow and elongated, with a knob at the distal end. In *Ceratobatrachus*, the phalanx is relatively broad at the basis, getting narrower towards the tip, and the tip ends in a small but distinct knob separated by a constriction that is about 1/3 as broad as the basis of the terminal phalanx. In *Dermatonotus*, the terminal phalanges are bent towards the ventral side. In *Euphlyctis*, the phalanx tip ends in a knob and the terminal phalanges of the toes are more elongated than the terminal phalanges of the fingers. In *Limnonectes* and *Fejervarya*, the phalanx tip ends in a knob separated by a constriction. In the two juvenile specimens of *Lithobates catesbeianus*, the phalanx is not broad, but relatively

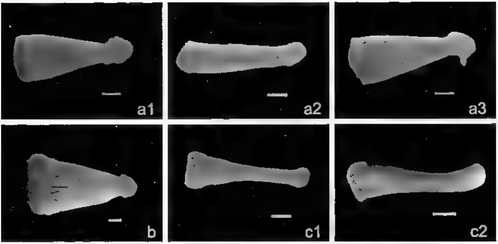


Fig. 3. – Scanning electron microscope pictures of terminal phalanges of third finger, all categorized in morphological state F. (a1-3) *Scaphophryne calcarata*, dorsal, lateral and ventral views; (b) *Ceratobatrachus guentheri*, ventral view; (c1-2) *Cacosternum boettgeri*, dorsal and lateral views. The scale bars represent 100 µm.

long, ending in a bulb. In *Microhyla*, the knob expands slightly in lateral direction, making this a vaguely mushroom-shaped form tending towards character state M. In *Nanorana*, the phalanx is relatively long and narrow, ending in a knob separated by a constriction. In *Occydozyga martensii*, the terminal phalanges distally end in a knob separated by a constriction. *Ptychadena schillukorum* is an exception among the species of *Ptychadena*, which are otherwise categorized within state E. The examined specimen of *Scaphophryne calcarata* has an anomaly on its lateral side on the distal end bulb. In *Scotobleps*, the terminal phalanges of the fingers are relatively long, not broad, and end in a small bulb. There are very slight lateral expansions, but these are too indistinct to be considered as representing a reduced form of state H. The terminal phalanges of the second and third toe have a hook-shaped morphology. The distal end of the first, fourth and fifth toe is rounded, but with lateral expansions, resulting in a mushroom-shaped form. In the species of *Sphaerotheca* and the two species of *Tomopterna*, in dorsal view, the terminal phalanx is broad at the basis. It has a clear bulb at the top, about half as broad as the basis. The phalanx is narrowest just before the knob, but a distinct constriction is lacking. In *Trichobatrachus*, the terminal phalanges of the fingers are cone-like and have a knob at the end. The terminal phalanges of the toes have a hook shape. In both specimens available, the hook-shaped morphology is present at all toes, however the biggest specimen has an extra, smaller hook on top of the hook-shaped toes. After dissolving the tissue with KOH, the extra, smaller hook appeared to be unconnected to the terminal phalanx (fig. 8a-b).

State G

The terminal phalanx is Y-shaped. Sometimes the two laterotermiinal projections are slightly curved towards each other. The following species are categorized in this state.

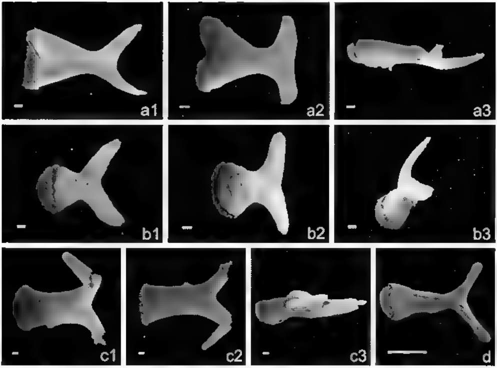


Fig. 4. Scanning electron microscope pictures of terminal phalanges of third finger, all categorized in morphological state G. (a1-3) *Anodonthyla montana*, dorsal, anteroventral and lateral views, (b1-3) *Phrynomantis bifasciatus*, dorsal and two ventral views (this species is categorized in state G, tending towards state J), (c1-3) *Rhacophorus dennysi*, ventral, dorsal and lateral views (both tips of the terminal phalanx broken), (d) *Polypedates otilophus*, dorsal view. The scale bars represent 100 µm.

Anodonthyla montana (fig. 4a); *Cophyla phyllodactyla*, *Heleophryne regia*; *Phrynobatrachus auritus*, *Phrynomantis bifasciatus* (fig. 4b) and *P. microps*; *Polypedates eques*, *P. maculatus* and *P. otilophus* (fig. 4d); *Rhacophorus dennysi* (fig. 4c) and *R. nigropalmatus*.

In *Anodonthyla*, the two projections are slightly curved towards each other. A constriction was visible towards the end of the two projections on the SEM picture. In *Heleophryne*, sometimes the two projections are slightly curved towards each other. In *Phrynobatrachus auritus*, the terminal projections are slightly less elongated. *Phrynomantis* has a slightly fishtail shaped terminal phalanx, reminding of *Chiromantis xerampelina* and *Hylarana (Amnirana)* cf. *albolabris*, which are categorized in state J. The anterodorsal view shows a T-shaped morphology wherein the distal end is more or less in a straight line and the two projections extend in lateral direction. In some of the (juvenile) specimens of *Polydepates eques* examined, a constriction is visible towards the end of the two projections, comparable to *Anodonthyla montana*. In *Rhacophorus*, the two projections are very narrow and in a straight line without curves.

State H

The terminal phalanges are T-shaped; at the distal end these form more or less a straight line. This state is similar to state G, only the two lateroterminal projections stretch away from each other in a more lateral direction. The following species are categorized in this state: *Batrachylodes elegans* and *B. vertebralis*; *Colostethus nubicola*; *Cophixalus darlingtoni* and *C. riparius*, *Dendrobates auratus*, *D. leucomelas* and *D. tinctorius*; *Oophaga pumilio*; *Epipedobates boulengeri*; *Ameerega silverstonei*, *Phrynobatrachus* cf. *versicolor*, *P.* cf. *werneri* and *P. cricogaster*, *Kaloula pulchra*; *Kassina decorata*; *Natalobatrachus bonebergi* (fig. 5a), *Petropedetes* sp. (fig. 5b); *Phrynodon* cf. *sandersoni* (fig. 5c-e); *Scaphiophryne marmorata*; *Staurois* sp.; *Arthroleptis* [*Schoutedenella*] sp.

In *Colostethus*, the projections (distance between their tips) are as extended as the length of the whole terminal phalanx. In *Epipedobates* and *Ameerega*, the projections are a little more extended than the whole length of the terminal phalanx. In the three species of *Phrynobatrachus* included here, the projections are less extended, but still more than in state M. *Kaloula* has a morphology different from others that are placed within this state. the two projections are not stretching away from each other but the phalanges are distally fan-shaped and ending in a straight line. Also *Kassina* has a different morphology, as the two projections are much broader than in the other taxa placed within this state. *Phrynodon* cf. *sandersoni* sometimes has up to two distal protuberances on the phalanx tip. The place of occurrence varies from centrally to just left or right of the centre. This seems to vary not only randomly between the specimens, but also between fingers and toes, between left and right hand or foot, and even between digits of a hand or foot. In *Scaphiophryne marmorata*, the phalanges are T-shaped, the distal end forms a more or less straight line. The two projections stretch away in lateral direction. In *Arthroleptis* [*Schoutedenella*] sp., the terminal phalanges have a slightly reduced T-shape. The distal end forms more or less a straight line. The projections are less elongated than in other species in state H.

State I

The terminal phalanges are slightly Y-shaped. The two lateroterminal projections are not as prolonged as in state G but rather short and more closely connected with each other. This state is found in all examined species of the genera *Boophis* (fig. 6b), *Gephyromantis*, *Guibemantis*, *Mantella* and *Mantidactylus* (fig. 6a) which all belong in the Madagascan family Mantellidae; and in the rhacophorid *Kurixalus verrucosus*.

In *Boophis boehmei*, *B.* cf. *madagascariensis*, *B.* sp. aff. *sibilans*, *B. idae*, *B. miniatus* and *B. tephraeomystax* (fig. 6b), on the ventral side a "bump" can be seen, with an incision in the center. This bump is present in many other species as well, but without incision. In *Gephyromantis webbi*, *Guibemantis bicalcaratus*, *G. flavobrunneus*, *Mantella aurantiaca*, *M. crocea*, *M. madagascariensis*, *Mantidactylus albofrenatus*, *M. grandidieri* and *M. ulcerosus*, the two projections are slightly curved to the lateral sides (fig. 6a). In *Kurixalus verrucosus*, the morphology is similar to that of *Boophis tephraeomystax* (fig. 6b).

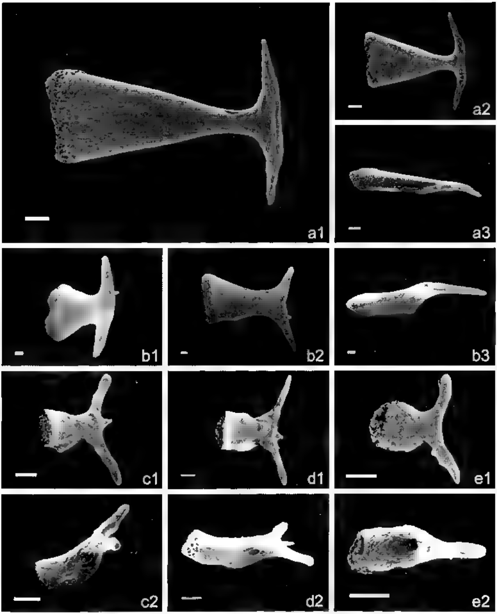


Fig. 5. Scanning electron microscope pictures of terminal phalanges of third finger, all categorized in morphological state H. (a1-3) *Nanorana* [illegible], dorsal, ventral and lateral views. (b1-3) *Petropedetes* sp., anteroventral, dorsal and lateral views (the small bump on top of the terminal phalanx of *Petropedetes* is probably dust, it does not represent a characteristic feature of this taxon). (c1-2) *Phr.* [illegible] cf. *andersoni*, dorsal and lateral views. (d1-2) *Phr.* [illegible] cf. *andersoni*, dorsal and lateral views of first and second finger. (e1-e2) *Ph.* [illegible] cf. [illegible], dorsal and lateral views of third finger. The occurrence and place of protuberances in this species varies, sometimes in the center and sometimes just left or right to the center. The number of processes varies from none to two. This seems to vary not only randomly between the specimens, but also between fingers and toes, between left and right hand or foot and even between digits of a hand or foot. The scale bars represent 100 µm.

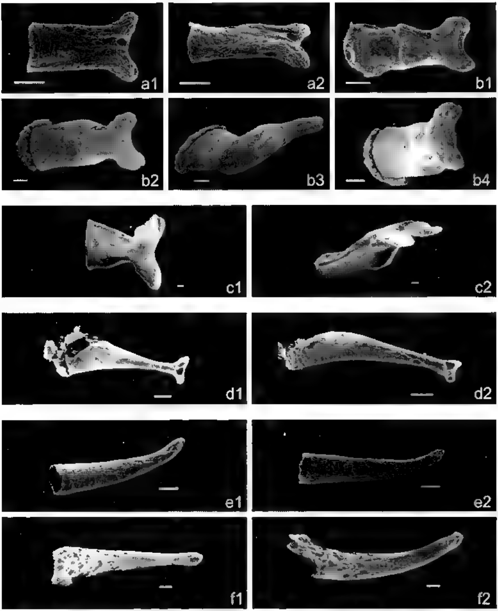


Fig. 6. – Scanning electron microscope pictures of terminal phalanges of third finger (unless otherwise mentioned), categorized in states I, J, K and L. (a1-2) *Mantidactylus ulcerosus*, dorsal and laterodorsal views, state I; (b1-4) *Boophis tephraeomystax*, ventral, dorsal and two anterodorsal views, state I; (c1-2) *Chiromantis xerampelina*, dorsal and lateral views, state J; (d1-d2) *Hyalinobatrachium fleischmanni*, ventral and lateral views, state K; (e1-e2) *Hymenochirus boettgeri*, posterolateral and lateral views, state L; (f1-f2) *Agalychnis callidryas*, ventral and lateral views, state L (even though the terminal phalanges on some of these SEM-photographs are broken, they still give a good view of their morphology in *Hyalinobatrachium* and *Agalychnis*). The scale bars represent 100 µm.

State J

This state is expressed in a Y-form and can be described as a fishtail-shape. It is similar to state G, but with the two lateroterminal projections being enlarged. It has only been observed in *Chiromantis xerampelina* (fig. 6c) and *Hylarana (Amnirana)* cf. *albolabris*.

State K

This state is reminiscent of a combination of states G and H, but with the terminal phalanges being strongly elongated and becoming very narrow towards the tip. It has only been observed in *Hyalinobatrachium fleischmanni* (fig. 6d)

State L

The terminal phalanx is very narrow and relatively long, ending in a pointed tip. The distal end is slightly curved towards the ventral side.

This form has been observed in the following species: *Agalychnis callidryas* (fig. 6f), *Hymenochirus boettgeri* (fig. 6e) and *Silurana tropicalis*. In this latter species, the terminal phalanx of the first, second and third toe have a hook-shaped morphology. The terminal phalanx tips of the fourth and fifth toe are rounded and slightly cone-shaped. The terminal phalanx tips of the fingers are also sharply pointed, but not bent towards the ventral side.

State M

The phalanges show rudiments of bifurcation distally. This state does not describe a well-defined single morphology but is rather somewhat of a "dumpbin" for species of intermediate states or where different morphologies are observed among digits. The observed morphologies are: (1) the distal end of the terminal phalanx cone-shaped with a knob at the distal end that bifurcates and has a distinct median notch; (2) the distal end rounded but with lateral expansions, resulting in a mushroom-shaped appearance; (3) a reduced T form.

The following species are categorized in this state: *Arthroleptis adelphus*, *A. adolfifriederici*, *A. poecilonotus*, *A.* sp. and *A. variabilis*; *Hylarana (Amnirana) lepus*, *Discoglossus montalentii*; *Discoglossus sardus*; *Gastrophryne* cf. *olivacea*; *Hylarana (Hydrophylax) galamensis*, *Hylarana (Hylarana) macrodactyla*, *Odorrana livida*, *Phlyctimantis verrucosus*, *Phrynobatrachus mababiensis*, *P. natalensis* and *P. werneri*; *Rana dalmatina* and *R. temporaria*; *Rhinoderma darwinii*; *Hylarana (Sylvirana) nigrovittata*, *Strongylopus grayii*; *Tachycnemis seychellensis*.

Due to the large variability in the detailed expression of this state, we here provide brief descriptions for all taxa exhibiting it. In *Arthroleptis adelphus*, *A. adolfifriederici*, *A. poecilonotus*, *A.* sp. and *A. variabilis*, the terminal phalanges shape varies. Distal ends can be bifurcated and have a distinct median notch, or have a mushroom-shaped morphology. In *Hylarana (Amnirana) lepus*, it bifurcates in lateral direction, mushroom-shaped. In *Discoglossus montalentii*, a strongly reduced T-shape is present both in fingers and toes. In *Discoglossus sardus*, the distal end of the terminal phalanx is cone-shaped with a knob at the distal end that bifurcates. There is no median notch, but the knob is not rounded either. The distal end slightly looks cubical In *Gastrophryne* cf. *olivacea*, two morphologies may occur on the same hand or foot without obvious order The distal end of the terminal phalanx can be: (1) cone-shaped with a distinct median notch; or (2) rounded (fig 7c). In *Hylarana (Hydrophylax) galamensis*, the terminal phalanx bends slightly towards the ventral side, ending in a bulb with two pointy tips, bifurcating in lateral direction From a anteroventral angle, the curve in the phalanx tips causes an incomplete view and shows a mushroom-shaped form, with a lowering between the two bifurcating tips (fig. 7g). In *Hylarana (Hylarana) macrodactyla* (two specimens), there is a highly reduced form of state H, bifurcating in lateral direction, without median notch In *Odorrana livida* (two specimens), the terminal phalanx tips bifurcate in lateral direction. One of the two specimens has a mushroom-shaped bulb towards the ventral side (fig. 7a), whereas the other specimen extends a bit more laterally and tends to look more like the reduced form of state H In *Phlyctimantis verrucosus*, two morphologies are observed: (1) the distal end of the terminal phalanx can be cone-shaped, bifurcating with a distinct median notch; or (2) the distal ends can be rounded, not shaped in any particular form. In *Phrynobatrachus mababiensis* (fig. 7e), *P natalensis* (fig 7d) and *P werneri* (fig. 7f), the phalanges are relatively narrow and elongated and with various terminal tip morphologies. From the lateral side, the phalanx of *P mababiensis* is straight with only the terminal tip bowing towards the ventral side. The broadened tip is divided into three parts on the anterior side, the central part of which is the shortest. The distal end of the terminal phalanx of *P natalensis* is cone-shaped with a knob at the distal end that bifurcates and has a distinct median notch. The phalanx of *P. werneri* is slightly T-shaped tending to state H, as the two short projections extend in lateral direction and bend slightly in anterior direction. The top makes a straight line. The projections do not extend as far as in state H. Other species within the genus *Phrynobatrachus* (*P auritus*, *P* cf. *versicolor*, *P.* cf. *werneri* and *P. cricogaster*) are placed in states G, H-M, H-M and H respectively In *Rana dalmatina*, the phalanx tip is mushroom-shaped. In *Rana temporaria*, the phalanx ends in a round mushroom-shaped bulb, which does not extend as much as other mushroom-shaped morphologies, tending towards state F. In *Rhinoderma darwinii*, the distal ends of both fingers and toes are rounded, but with lateral expansions, resulting in a mushroom-shaped form In *Hylarana (Sylvirana) nigrovittata*, the distal end is in a straight line and bifurcates in lateral direction A highly reduced form of state H is observed in *Strongylopus grayii*. the distal ends are rounded with lateral expansions, resulting in a mushroom-shaped form (fig 7b) In *Tachycnemis seychellensis* as in *Phlyctimantis*, two morphologies are observed (1) the distal end of the terminal phalanx is cone-shaped, bifurcates and has a distinct median notch; and (2) the distal end is rounded, not shaped in any particular form.

MAJOR MORPHOLOGICAL GROUPS

Most of the different states defined above can be summarized in three major morphological groups, defined below States B and C could not be placed in any of these groups, because their morphology is too aberrant States D and M do not clearly fit in any of the groups either, and are possibly reduced forms of one of the other states.

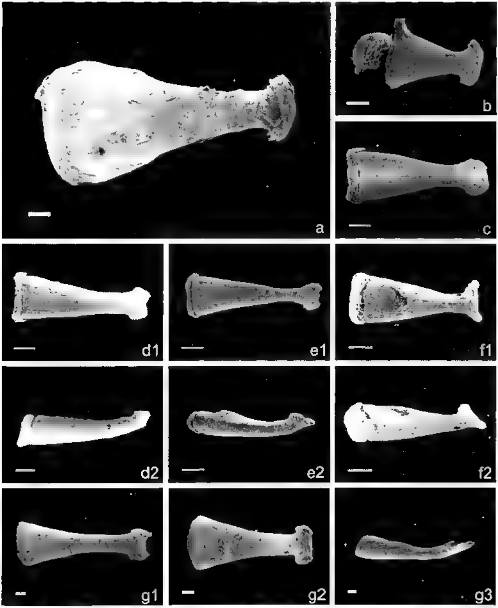


Fig. 7. Scanning electron microscope pictures of terminal phalanges of third finger (unless otherwise mentioned in the following), all categorized in state M. (a) *Odorrana livida*, ventral view, (b) *Strongylopus grayii*, dorsal view, (c) *Gastrophryne* cf. *olivacea*, dorsal view, (d1-2) *Phrynobatrachus natalensis*, dorsal and lateral views, (e1-2) *Phrynobatrachus mababiensis*, fourth toe, dorsal and lateral views, (f1-2) *Phrynobatrachus werneri*, fourth toe, ventral and ventrolateral views, (g1-3) *Hylarana (Hydrophylax) galamensis*, dorsal, ventral and lateral views. The scale bars represent 100 µm.

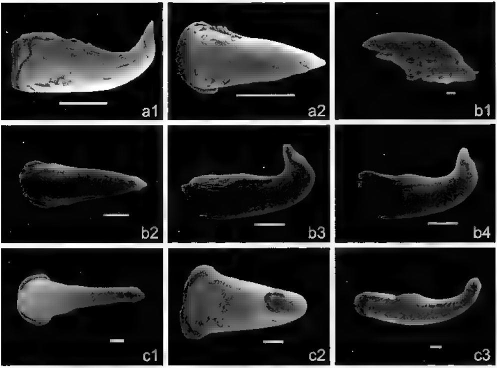


Fig. 8. Scanning electron microscope pictures of terminal phalanges of fourth toe categorized as hook-shaped morphology (a1-2) *Trichobatrachus robustus* (ZFMK 68850), lateral and dorsal views, (b1) *Trichobatrachus robustus* (ZFMK 68851, hook on top of the terminal phalanx), lateral view, (b2-4) *Trichobatrachus robustus* (ZFMK 68851), dorsal, lateroventral and lateral views (the morphology of the third finger of *Trichobatrachus robustus* is categorized in state F), (c1-3) *Ptychadena mascareniensis*, dorsal, ventral and lateral views. The scale bars represent 100 µm.

Morphological group I

Pointed terminal phalanx tips, states A and L: *Afrixalus*, *Agalychnis*, *Fejervarya* (also state F), *Heterixalus*, *Hymenochirus*, *Hyperolius*, *Leptodactylodon*, *Leptopelis*, *Megophrys*, *Occidozyga* (also state F), *Phyllomedusa* and *Silurana*.

Morphological group II

Rounded and relatively broad terminal phalanx tips, states E and F: *Aglyptodactylus*, *Astylosternus*, *Bombina*, *Breviceps*, *Cacosternum*, *Calluella*, *Ceratobatrachus*, *Dermatonotus*, *Discoglossus*, *Euphlyctis*, *Fejervarya* (also state A), *Hemisus*, *Hoplobatrachus*, *Hyla*, *Laliostoma*, *Limnonectes*, *Lithobates*, *Microhyla*, *Nanorana*, *Occidozyga* (also state A), *Platymantis*, *Pseudophryne*, *Ptychadena*, *Quasipaa*, *Scaphiophryne brevis* and *S. calcarata*, *Scotobleps*, *Sphaerotheca*, *Tomopterna* and *Trichobatrachus*.

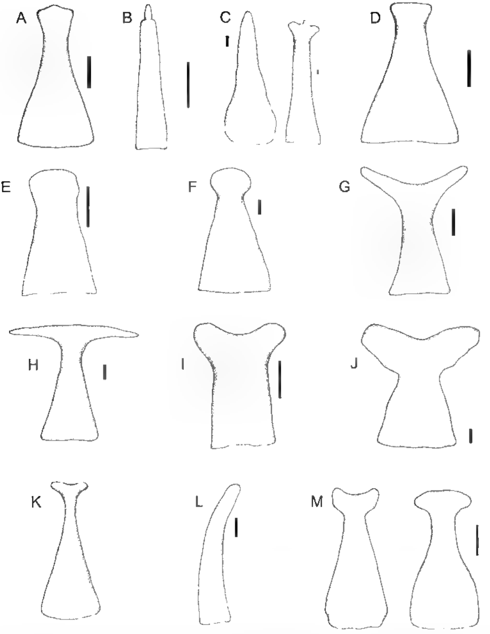


Fig 9 Character states of terminal phalanx shape as distinguished in the present work All drawings represent the third finger, except for the left drawing of character state C, which represents the fourth toe The character state M includes phalanges with rudiments of distal bifurcation, and comprises different morphologies. Here, two examples are given of this character state The morphologies can differ dependent on the observer's angle of observation This is especially true for the drawing of character state A What seems to be a slightly pointed head, is in fact a small bulb curving towards the ventral side (fig. 1a) The distal end of this bulb is rather flat than pointed The scale bars represent 100 µm

Source MNHN, Paris

Morphological group III

Bifurcated terminal phalanx tips, states G, H, I, J and K: *Ameerega*, *Anodonthyla*, *Batrachylodes*, *Blommersia*, *Boophis*, *Chiromantis*, *Colostethus*, *Cophixalus*, *Cophyla*, *Dendrobates*, *Epipedobates*, *Gephyromantis*, *Guibemantis*, *Heleophryne*, *Hyalinobatrachium*, *Hylarana* [subgenus *Amnirana*], (*Kaloula*), (*Kassina*), *Mantella*, *Mantidactylus*, *Natalobatrachus*, *Oophaga*, *Petropedetes*, *Phrynobatrachus* (some specimens in state M), *Phrynodon*, *Phrynomantis*, *Polypedates*, *Rhacophorus*, *Scaphiophryne marmorata*, *Arthroleptis* [*Schoutedenella*], *Spinomantis* and *Staurois*.

CONSENSUS PHYLOGENY, CHARACTER TRACING AND CHARACTER CORRELATION

The systematics of ranoid frogs are still in a flux, but recent molecular work has clarified much of their basal phylogeny We summarized molecular trees based on multi-gene analyses as published by BIJU & BOSSUYT (2003), ROELANTS et al. (2004), HOEGG et al. (2004), VAN DER MEIJDEN et al (2004, 2005) and VENCES et al (2003). We produced an informal supertree by manually superimposing these trees with molecular trees of deep amphibian relationships (SAN MAURO et al., 2005; ROELANTS & BOSSUYT, 2005), and considered nodes that received high support (Bayesian posterior probabilities > 95 % or bootstrap support values > 70 %) in at least one of the analyses and were not contradicted by highly supported alternative topologies in other analyses. A few additional aspects of the topologies were resolved following the analysis of FROST et al. (2006), although these authors did not provide bootstrap values which would have given a directly comparable measure of support to other analyses. Because of the limitations in including phalanx shape assessments published by other authors, we only included in the tree those genera for which terminal phalanx data were gathered in the present study. The resulting consensus tree is shown in fig. 10-11 Tracing character state transformations based on our original character states on this tree (not shown) required a minimum of 52 transformations and resulted in a consistency index (ci) of 0.38 and a retention index (ri) of 0 36. Tracing the three major groups of character states (not shown) required a minimum of 19 transformations and yielded values of ci/ri values of 0 11 and 0.48.

Reconstruction of ancestral states was ambiguous on these trees in most cases. In order to test for a possible correlation between habits and distal enlargement of the terminal phalanx, we divided the observed states in two major groups, namely (1) those without a distinct distal enlargement as in morphological groups I and II above (plus states D and M), and (2) those with a distinct Y-shaped, mushroom-shaped or T-shaped distal enlargement, as in morphological group III above This character resulted in ci/ri values of 0.06 and 0 46, and a tree length of 16 transformations. Character tracing supported distally non-enlarged phalanges as the ancestral state in most major clades and supported an independent origin of distally enlarged phalanges in 12 clades (fig 10) In at least two cases a reversal was indicated, and two further transformations could not be unambiguously identified as either origin or reversal

We further grouped the genera studied grossly by their habits in non-climbing species (terrestrial, semi aquatic and aquatic species) and climbing species (including arboreal, semi arboreal and rock-dwelling taxa) This character resulted in ci/ri values of 0.05 and 0 40, and a tree length of 19 transformations. Non-climbing habits were identified as ancestral and 11 independent origins of climbing habits were identified (fig 11). Two reversals to non-climbing behaviour and five transformations of uncertain direction were further identified. Of the 11 origins of climbing, six coincided precisely with the origin of distally dilated phalanges. In several cases, this correlation seems obvious: (1) *Aglyptodactylus* and *Laliostoma*, clearly embedded in the Mantellidae/Rhacophoridae clade, are the most terrestrial mantellids and the only representatives in this family without distally enlarged terminal phalanges; (2) the most clearly rock-dwelling or scansorial ranoids, such as *Staurois*, *Natalobatrachus*, *Phrynodon* and *Petropedetes*, all have distally enlarged phalanges, (3) in *Scaphiophryne*, the one included species with enlarged finger disks and at least occasional climbing behaviour, *S. marmorata*, has distinct T-shaped phalanges, whereas the purely terrestrial species do not show any enlargement. Nevertheless, several striking counter examples exist as well, indicating that this correlation is certainly not an obligatory one: (1) the fully arboreal hylids show no distal enlargement, and (2) the same is true for the arboreal hyperoliids and leptopelines (paradoxically, except for the largely terrestrial *Kassina*).

For the concentrated changes test of character correlation as implemented in MacClade (using 10,000 simulations), it is necessary to trace ancestral states of dependent as well as independent variable as precisely as possible. In order to allow for unambiguous reconstructions, we therefore resolved the polytomies in our phylogeny as follows: (1) among microhylids, positioning *Phrynomantis* as most basal and gastrophrynines sister to microhylines; (2) among mantellines, placing boophines as most basal. It is highly unlikely that any alternative resolution of these polytomies would have affected the outcome of the concentrated changes test in a relevant way. Using *Deltran* character tracing, and under the null hypothesis that gains and losses are randomly distributed, the probability of observing, out of 13 gains and 4 losses, of the character state "bifurcated", the observed 7 and 0 (defined as more than 6 and less than 1), respectively, on branches distinguished by the character state "climbing", was lower than 0.005. Under *Acctran* reconstruction of ancestral states, 11 gains and 6 losses of bifurcated terminal phalanges were observed, 7 and 1 of which occurred in subclades characterized by a climbing character state ($P < 0.005$). Under MINSTATE and MAXSTATE simulations, the significances decreased, but the null hypothesis of randomly distributed changes (no correlation) was still significantly rejected ($P < 0.05$) in all cases.

DISCUSSION

COMPARISON WITH PREVIOUS STUDIES

In ranoid frogs, four authors (LIEM, 1970; CLARKE, 1981, DREWES, 1984, SCOTT, 2005) have analysed the shape of terminal phalanges in detail and defined character states to be analysed in a phylogenetic context.

LIEM (1970), in a study of Old World treefrogs (currently in the Hyperoliidae, Rhacophoridae and Mantellidae), recognized four states of the terminal phalanx (tab. 1), three of which compare directly to states E/F, G and I here. LIEM's (1970) state 1 compares to a

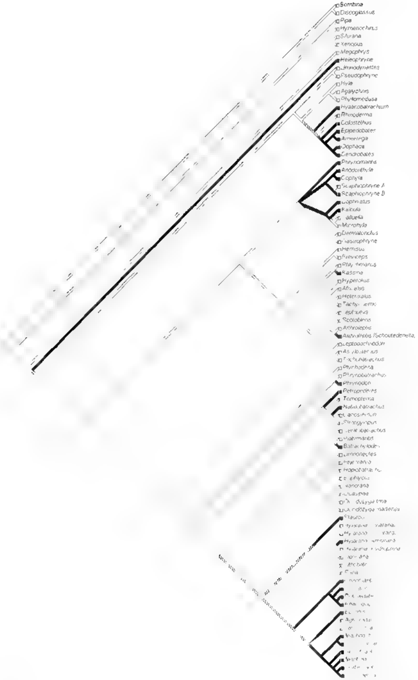


Fig. 10. — Phylogenetic tree of the taxa studied, based on informal merging of recent molecular phylogenies, with character tracing of bifurcated (black, character states G, H, I, J and K) vs. non-bifurcated (white, other character states) phalanx shape. Hatched branches indicate ambiguous reconstruction.

Source : MNHN, Paris

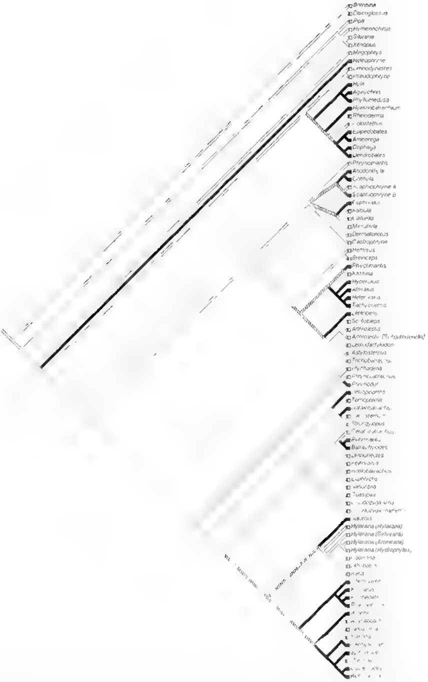


Fig. 11. Phylogenetic tree of taxa studied, based on informal merging of recent molecular phylogenies, with character tracing of climbing (black) vs. non-climbing (white) habits. Hatched branches indicate ambiguous reconstruction. Note that it is very difficult to clearly define these character states. The assignations used here are meant to refer only to the species studied by us, and in some cases certainly are controversial: this refers for instance to the definition of *Heleophryne* as (rock-) climbing, and of the studied species of *Hylarana* as non-climbing although they can regularly be found in the vegetation. Assigning alternative character states to these taxa, however, would not have resulted in relevant changes of the results of the analysis.

Table 1. Character states of terminal phalanx shape as used by Liem (1970) (first column) and their equivalents as defined here (last column).

State	State description	Compares to
0	Obtuse terminal phalanx, the distal end is simple or a rounded knob	States E and F
1	Claw-shaped terminal phalanx; pointed and curved downwards	Hook-shaped toe morphology
2	Bifurcate terminal phalanx; the distal end is slightly bifurcate but not pointed, and the length of each branch is less than the width of the phalanx	State I
3	Y-shaped terminal phalanx; the distal ends are pointed and the length of each branch is longer that the width of the phalanx	State G

hook-shaped morphology found in the toes of *Trichobatrachus robustus*, *Ptychadena bibroni*, *Astylosternus montanus*, *Scotobleps gabonicus* and *Silurana tropicalis*. Liem's (1970) general observation of taxa currently in the Rhacophoridae and Mantellidae having Y-shaped or bifurcated phalanges corresponds well with the results obtained here.

Clarke (1981) examined African species today classified in the Ranidae, Dicroglossidae, Ptychadenidae and Pyxicephalidae (Frost et al., 2006) and recognized seven different states of terminal phalanx shape. Clarke's (1981) states 1, 2 and 5 are reduced forms and were subsumed as state M in our study (tab. 2); state 0 compares to our state F and was found in species of Ranidae, in agreement with our observations of state M in *Hylarana (Hylarana) macrodactyla*, state 1 is comparable to our state M and was found in *Hylarana (Hydrophylax) galamensis* and *Strongylopus*, state 2 is also comparable with our state M and was found in *Aubria*, some species of *Conraua*, *Hoplobatrachus occipitalis* and *Pyxicephalus*. We did not study any of these taxa, and the precise form of this state according to Clarke's (1981) drawings was not observed by us in any other specimen, state 3, seen by Clarke (1981) as extreme expression of state 2, was only observed in *Conraua beccarii* which we did not study here; state 4 is described as reduced and almost cone-like, and appears to best compare to our state E, it was found by Clarke (1981) in *Tomopterna*, *Hildebrandtia* and *Pyxicephalus*, whereas we categorized *Tomopterna* in state F. Clarke (1981) used a juvenile specimen of *Pyxicephalus adspersus* with incomplete ossification of the skeleton, which lead to doubt in showing state 2 or 4, state 5, comparable to state M in our study, was found in *Lanzarana largeni* (not studied here); state 6 (comparable to our states A and L) was found in *Ptychadena* only, but according to our results, species of *Ptychadena* are characterized by a tendency towards a small terminal bulb and are therefore categorized in state E. Only *Ptychadena floweri* was not categorized in state E, but in state F. The pointed, dorsoventrally curved distal end in this species compares to a reduced form of a hook-shaped morphology, observed in this study in the phalanges of the toes of *P. bibroni*.

Drewes (1984) analysed the terminal phalanges of the third finger, mainly in hyperoliids and leptopelines, but for comparative purposes also in other ranoids. He distinguished four states (tab. 3). State 0, from the drawings and descriptions provided, is comparable to the hook-shaped morphology, which in this study has only been observed in toes. State 1 compares to morphological group II, consisting of states E and F. The slightly notched

Table 2. Character states of terminal phalanx shape as used by CLARKE (1981) (first column) and their equivalents as defined here (last column)

State	State description	Compares to
0	Distal ends of terminal phalanges of fingers and toes simple, rounded, knob-like	State F
1	Distal ends of terminal phalanges of fingers and toes bifurcate (have a distinct median notch, state 2 of LIEM, 1970)	State M
2	Distal ends of terminal phalanges of fingers and toes rounded, but with lateral expansions, making the outline of the distal phalanx "mushroom-shaped" in appearance (no median notch)	State M
3	Distal ends of terminal phalanges of fingers simple, knob-like or as state 2, toes slightly T-shaped; the anterior distal border of the phalanx perpendicular to the axis (no median notch)	Reduced form of state H
4	Terminal phalanges of fingers and toes reduced, almost cone-like	State E
5	Fingers with expanded distal ends to terminal phalanges, phalanx appearing almost "dumbbell-shaped" (especially on third and fourth fingers); toes similar to state 4	State M
6	Distal ends of terminal phalanges of fingers and toes fairly pointed, curved dorsoventrally	States A and L

Table 3. Character states of terminal phalanx shape as used by DREWES (1984) (first column) and their equivalents as defined here (last column)

State	State description	Compares to
0	Terminal phalanx long, slender, and claw-shaped; curved ventrally and tapered evenly to a point.	Hook-shaped toe morphology
1	Terminal phalanx long, slender and peniform; a noticeable constriction present near tip; tip oval, but not pointed; phalanx may be slightly curved	Morphological group II (states E and F)
2	Terminal phalanx short, obtuse, and unmodified or with the tip slightly notched or emarginate	State M and morphological group I (states A and L), state M comprises different forms where the slightly notched morphology belongs; morphological group I can account for the unmodified tip
3	Tip bifurcate, each branch longer than width of phalanx just proximal to bifurcation	Morphological group III (state H)

morphology of state 2 compares to state M, whereas the unmodified tips fit state A and L (morphological group I). State 3 compares to morphological group III, more specifically to state H. Of the species categorized in state 0 by Drewes (1984), we studied *Heterixalus madagascariensis*, *Hyperolius argus*, *Leptopelis bocagii* and *L. modestus*. All were categorized in our state A, as well as other species studied within these genera. Of the species categorized in state 1 by Drewes (1984), we studied the following species: *Afrixalus fornasini*, *A. fulvovittatus*, *Hyperolius nasutus*, *H. pusillus*, *H. tuberilinguis* and *Tachycnemis seychellensis*. Except for *Tachycnemis seychellensis*, which was categorized in our state M, all were categorized in our state A. Of the species categorized in state 2 by Drewes (1984), we studied *Kassina decorata*, which was placed in our state H, and *Phlyctimantis verrucosus*, which was placed in our state M. We did not study any of the species categorized in state 3 by Drewes (1984). We assume that the contradictions between the assignation of species to morphological states, between Drewes (1984) and our analysis, does not indicate true polymorphisms but are rather due to differences in interpretation.

Scott (2005) examined a large number of ranoid species osteologically and composed a data matrix of morphological and molecular characters for phylogenetic analysis. She distinguished between the terminal phalanx shape of the fourth finger and the fourth toe, defining three states within the finger morphology (tab. 4) and seven states within the toes (tab. 5). Here a comparison will be made for finger phalanx morphology.

State 0 of Scott (2005) is bifurcate, T- or Y-shaped, and compares to our morphological group III, which consists of states G, H, I, J and K. Of the taxa categorized in Scott's (2005) state 0, the following species were also analysed in the present study: *Natalobatrachus bonebergi*, *Batrachylodes vertebralis*, *Phrynobatrachus cricogaster*, *Phrynodon* cf. *sandersoni*, *Petropedetes* sp. [*P. cameronensis*, *P. natator*, *P. newtoni* and *P. parkeri* studied by Scott (2005)] and *Staurois* sp. [*S. natator* studied by Scott (2005)], all categorized in our state H, *Hylarana (Amnirana)* cf. *albolabris* and *Chiromantis xerampelina*, placed in our state J; *Phrynomantis bifasciatus*, placed in state G, tending to state J; *Phrynobatrachus natalensis* and *Hylarana (Hydrophylax) galamensis*, placed in our state M; *Mantella aurantiaca*, placed in our state I.

State 1 of Scott (2005) is knob-like and simple, and compares to our morphological group II, which consists of states E and F. Of the species categorized in Scott's (2005) state 1, the following species were also analysed in the present study: *Afrixalus fornasini*, *Hyperolius marmoratus* and *Leptopelis* cf. *mossambicus*, placed in our state A; *Hemisus marmoratus*, *Breviceps mossambicus* and *Platymantis corrugatus*, placed in our state E; *Cacosternum boettgeri*, *Trichobatrachus robustus* and *Scotobleps gabonicus*, placed in our state F, although the latter two species showed a hook-morphology of toe phalanges; *Arthroleptis variabilis*, placed in our state M.

State 2 of Scott (2005) is sharply pointed and slightly elongated. The elongation compares to our state L, whereas the sharply pointed morphology matches the hook-shaped morphology found in the terminal phalanges of the toes (but not the fingers) of *Trichobatrachus robustus*, *Ptychadena bibroni*, *Astylosternus montanus*, *Scotobleps gabonicus* and *Silurana tropicalis*. Of the species categorized in state 2 of the finger morphology by Scott (2005), we studied *Ptychadena mascareniensis*, which we placed in state E, and *Strongylopus grayii* which we placed in state M.

Table 4 Character states of terminal phalanx shape of digit IV of hand as used by SCOTT (2005) (first column) and their equivalents as defined here (last column).

State	State description	Compares to
0	Bifurcate, T- or Y shaped	States G, H, I, J and K (morphological group III)
1	Knob-like, simple	States E and F (morphological group II)
2	Sharply pointed, slightly elongated	Elongated state L; sharply pointed: hook-shaped morphology

Table 5. Character states of terminal phalanx shape of digit IV of foot as used by SCOTT (2005) (first column) and their equivalents as defined here (but largely refering to fingers: last column).

State	State description	Compares to
0	Large T-shaped	State H
1	Small T- or Y-shaped	States G, H and (I)
2	Simple or only slightly dilated	State M
3	Long, sharply pointed	State N
4	Y-shaped, arms bearing flattened ovate flanges	State J
5	Pointed, truncated (short) to triangular, tip may be a small globule	States E and F
6	Long, sharply pointed, as in state 3, but tip separated from the body of terminal phalanx and bent sharply downwards (may or may not perforate the integument in life)	The extra hook separated from the rest of the phalanx, similar to the observation reported here in one specimen of *Trichobatrachus robustus*

SCOTT (2005) referred to *Phrynodon* having T-shaped tips (according to BLOMMERS-SCHLÖSSER, 1993), whereas she observed only Y-shaped tips herself. The SEM pictures in our study (fig. 5c-e) show a morphology in-between the two forms, with protuberances on top of the tips.

One further aspect that requires discussion is the identification reliability of the specimens studied. Many species of ranoids, especially small-sized African and Asian species, are notoriously difficult to identify to species, sometimes even to genus. We are confident in our identification of mantellid, brevicipitid, microhylid and pyxicephalid species, but this is much less true for various phrynobatrachid, ptychadenid, arthroleptid or rhacophorid taxa, several of which were obtained from the pet trade without verified locality data. Genus attribution of all specimens studied herein is reliable, and possible misidentifications will not affect our major conclusions. However, when comparing detailed data for single species among studies, this potential source of error, in our study as well as in published works, needs to be considered.

HOMOPLASY AND ECOLOGICAL CORRELATES OF PHALANX MORPHOLOGY

Several authors have reported differences between phalanges of fingers and toes, and also among fingers or toes. DREWES (1984) found little variation in this respect in the species examined, but restricted his analysis to the third finger based on the work of HEYER (1975) in hyloid frogs at the time considered to be in the family Leptodactylidae (now partitioned; FROST et al., 2006). HEYER (1975) found variation of terminal phalanx shape from digit to digit. CLARKE (1981) has also noted that the phalanx morphology on toes and fingers does not necessarily correspond to each other. Any one of the states he distinguished varies in degree on the different digits of a limb. He noted that in general a given state is best expressed on the third and fourth fingers on the hand, and the third, fourth and fifth toes on the foot. Our observations confirm that the general phalanx morphology of a species is best expressed in the longest digits available, which usually are the third finger and the fourth toe.

Altogether the comparisons reported above indicate that scoring character states of terminal phalanx shape in frogs is a difficult endeavour, and along with FABREZI (1996) we conclude that this character is strongly affected by homoplasy. The number of states distinguished appears to depend on which groups of ranoids are studied, and certainly is also affected by subjective decisions of the different researchers. LIEM (1970) focused on rhacophorids, mantellids and hyperoliids, with some additional taxa as outgroups, and distinguished four states; DREWES (1984) studied mainly hyperoliids and leptopelines, and distinguished four states; CLARKE (1981) studied representatives of dicroglossids, ptychadenids, pyxicephalids and dicroglossids, and distinguished seven states. SCOTT (2005) studied most lineages of ranoids and distinguished three character states for finger phalanx shape, and seven character states for toe phalanx shape. In the present study we used SEM to better visualize the phalanx morphology and partly arrived at categorizations different from those of previous workers. However, in many cases, especially when terminal structures are weakly expressed, it is very difficult to provide a clear categorization and distinction between clear-cut states, a dilemma also noted by CLARKE (1981) and FABREZI (1996). In addition, ontogenetic artefacts may more commonly have the power to obscure genetically determined (and hence phylogenetically relevant) underlying morphology in such "reduced" states where the diagnostic shape is not marked by distinctive protruding elements. We do not expect sexual dimorphism to occur in this and most other osteological characters, but such a potential influence remains largely unstudied. For these methodological reasons alone, and in line with the conclusion of CLARKE (1981), the value of the morphology of terminal phalanges to infer phylogenies must be seen as very limited.

A further issue is whether terminal phalanges undergo rapid adaptive modifications and can therefore mask rather than resolve phylogenetic relationships. Several authors correlated terminal phalanx morphology with habitat and habits. DREWES (1984) hypothesized that this character can be explained by the frog's habitat, and that the different states may constitute specialisations for muscle insertions. LIEM (1970) noted that modifications of the terminal phalanx were present in most arboreally adapted species, and CLARKE (1981) assumed that terminal phalanges often undergo adaptive modifications.

The survey and comparative analysis presented here indicate, on one hand, an important phylogenetic component in terminal phalanx morphology. For example, all species of the subfamilies Boophinae and Mantellinae in the family Mantellidae examined (Liem, 1970; Vences et al., 2002; our data) have a similar, slightly Y-shaped bifurcated phalanx shape (our state I), although the Mantellidae are a rather old group that probably split from the Rhacophoridae in Cretaceous to Paleocene times (Bossuyt & Milinkovitch, 2001; Vences et al., 2003), and although especially mantellines are ecologically and morphologically very diverse, containing climbing as well as largely terrestrial frogs (Glaw & Vences, 2006). A similar case can be made for several other groups, such as the Hyperoliidae which almost all have non-bifurcated phalanges. A phylogenetic component is also obvious from the fact that several character states were identified in the few non-ranoid taxa examined here which were not found in any of the vast number of ranoids studied.

On the other hand, our data also provide the first significant evidence for shifts in phalanx morphology in concert with shifts in habits of the frogs. Such an analysis is made difficult by the plethora of different character states observed. We therefore decided to study a single pattern, terminal bifurcation of phalanx, where a reasonable working hypothesis could be drawn and tested: arboreal and rock dwelling climbing frogs have usually evolved (phylogenetically independently; Ohler & Dubois, 1989) enlarged disks of fingers and toes, and an enlarged terminal phalanx may be useful as internal support for this disk, or as attachment for muscles that increase disk mobility for improved climbing. A correlation of these characters with the presence of an intercalary element between terminal and subterminal phalanges of fingers and toes, and of this element with climbing habits, has already been found by Manzano et al. (2007). By coding terminal phalanx shape and habits each as binary characters (terminal enlargement of phalanx by bifurcation, vs. no such distinct enlargement; and climbing vs. not climbing) we could apply a statistical test and reject a stochastic distribution of both characters along the phylogeny. This indicates that indeed terminal phalanx bifurcation evolved multiple times in concert with climbing behaviour, but more sophisticated analyses are necessary to better understand this evolutionary process. Since bifurcation differs in several metric variables (angle of protrusion of lateroterminal processes, and their length and width), and arboreal and rock-dwelling frogs differ in the degree of climbing (e.g., some scansorial frogs climb only at night whereas other frogs leave the trees only for breeding), it is in principle possible to perform a quantitative comparative analysis along a phylogeny. Other factors could be taken into account by multivariate approaches, such as the size of the terminal finger disks, the presence of intercalary elements and the structure of digit muscles, which may functionally correlate with terminal phalanx shape (Manzano et al., 2007). We are convinced that more in-depth descriptive studies of morphological character states in combination with character tracing along well-supported molecular phylogenies will be highly informative to understand their ecological correlates and adaptive value. Along with Scotland et al. (2003), but acknowledging the criticims of Jenner (2004) and Wiens (2004) to a generalization of this approach, we believe in the usefulness of detailed analysis of particular morphological characters, in this case in anuran osteology. In contrast to uncritical studies that aim to add a maximum number of morphological characters to data matrices for phylogenetic analyses, such detailed and focused morphological analyses are more promising. They are required to identify diagnostic and phylogenetically informative characters for major anuran clades which are badly needed to reliably assign fossil forms to evolutionary lineages. And they will contribute to the long-neglected field of anuran functional anatomy by drawing hypotheses on possible adaptive significances of particular character states.

ACKNOWLEDGEMENTS

We are indebted to numerous friends and colleagues who allowed examination and clearing and staining of material collected by them or held in museum collections under their care, in particular Franco Andreone (MRSN, Torino), Wolfgang Böhme (ZFMK, Bonn), Alain Dubois and Annemarie Ohler (MNHN, Paris), Frank Glaw (ZSM, München), Berthus van Tuijl (ZMA, Amsterdam), Linda Trueb (Laurence) and Thomas Ziegler (Cologne) Furthermore we are grateful to Jan van Arkel, Dirk Platvoet and Saskia A.F Marijnissen for their technical assistance and moral support

REFERENCES

Biju, S. D & Bossuyt, F , 2003 New frog family from India reveals an ancient biogeographical link with the Seychelles. *Nature*, **425**. 711-714

Blommers-Schlosser, R. M A., 1993 - Systematic relationships of the Mantelllinae Laurent 1964 (Anura Ranoidea). *Ethol Ecol Evol.*, **5**: 199-218

Bossuyt, F & Milinkovitch, M. C , 2000 Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *Proc natl Acad Sci USA*, **97**· 6585-6590.

----- 2001 Amphibians as indicators of Early Tertiary "out-of-India" dispersal of vertebrates. *Science*, **292**. 93-95

Channing, A , 1989 A re-evaluation of the phylogeny of Old-World treefrogs. *S Afr J. Zool* , **24**: 116-131.

Clarke, B T , 1981 Comparative osteology and evolutionary relationships in the African Raninae (Anura Ranidae). *Monit zool. ital* , (n.s.), **15** (suppl.): 285-331.

Deckert, K , 1938 Beitrage zur Osteologie und Systematik ranider Froschlurche *Sber Ges. Naturf Freunde Berlin*: 127-184

Dingerkus, G & Uhler, L D., 1977 Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technol.*, **52**: 229-232

Drewes, R. C , 1984 A phylogenetic analysis of the Hyperoliidae (Anura): treefrogs of Africa, Madagascar, and the Seychelles Islands. *Occ. Pap. Calif Acad. Sci* , **139**: 1-70

Dubois, A , 1992 Notes sur la classification des Ranidae (Amphibiens Anoures) *Bull mens. Soc linn. Lyon*, **61**: 305-352.

----- 2005 *Amphibia Mundi*. 1.1 An ergotaxonomy of recent amphibians. *Alytes*, **23** 1-24

Emerson, S B., 1983 Functional analysis of frog pectoral girdles. The epicoracoid cartilages. *J. Zool* , London, **201**· 293-308

----- 1986. Convergence and morphological constraint in frogs variation in postcranial morphology. *Fieldiana Zoology*, **43**: 1-19

Fabrezi, M , 1996 Las falanges terminales en la clasificacion de los anuros. *Cuad Herpet* , **10**· 1-9

Fabrezi, M & Alberch, P., 1996 The carpal elements of anurans. *Herpetologica*, **52** 188-204

Fabrezi, M & Emerson, S., 2003 Parallelism and convergence in anuran fangs. *J. Zool* , London, 260 41-51

Frost, D. R., Grant, T , Faivovich, J , Bain, R. H , Haas, A , Haddad, C. F. B , de Sa, R. O , Channing, A., Wilkinson, M , Donnellan, S C., Raxworthy, C. J., Campbell, J. A., Blotto, B L , Moler, P Drewes, R C , Nussbaum, R A , Lynch, J D , Green D M & Wheeler, W C., 2006. – The amphibian tree of life. *Bull. Amer Mus. nat Hist* , 297. 1-370

Glaw, F , Hoegg, S & Vences, M , 2006 Discovery of a new basal relict lineage of Madagascan frogs and its implications for mantellid evolution. *Zootaxa*, **1334** 27-43

Glaw, F & Vences, M 2006 Phylogeny and genus-level classification of mantellid frogs. *Org Divers Evol* , **6**. 236-253

Heyer, W. R., 1975. A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. *Smith. Contr. Zool.*, **199**: 1-54.

Hoegg, S., Vences, M., Brinkmann, H. & Meyer, A., 2004. – Phylogeny and comparative substitution rates of frogs inferred from sequences of three nuclear genes. *Mol. Biol. Evol.*, **21**: 1188-1200.

Jenner, R. A., 2004. – Accepting partnership by submission? Morphological phylogenetics in a molecular millennium. *Syst. Biol.*, **53**: 333-342.

Laurent, R. F., 1940. – Contribution a l'ostéologie et à la systematique des Ranides africains. Premiere note. *Rev. Zool. Bot. afr.*, **34** (1): 74-96.

----- 1941*a*. Contribution à l'osteologie et à la systématique des Ranides africains. Deuxième note. *Rev. Zool. Bot. afr.*, **34** (2): 192-234.

----- 1941*b*. Contribution a l'osteologie et à la systématique des Rhacophorides africains. Première note. *Rev. Zool. Bot. afr.*, **35** (1): 85-110.

----- 1943*a*. Sur la position systématique et l'osteologie du genre *Mantidactylus* Boulenger. *Bull. Mus. r. Hist. nat. Belg.*, **19** (5). 1-8.

----- 1943*b*. - Contribution à l'ostéologie et à la systématique des Rhacophorides non africains. *Bull. Mus. r. Hist. nat. Belg.*, **19** (28). 1-16.

----- 1944. – Contribution à l'ostéologie et à la systématique des Rhacophorides africains. Deuxième note. *Rev. Zool. Bot. afr.*, **38** (1-2): 110-137.

Laurent, R. F. & Fabrezi, M., 1985. Le carpe des Arthroleptinae. *Alytes*, **4**. 85-93.

----- 1990. – Further data on carpal structure in ranoid frogs. *Alytes*, **8**: 41-50.

Leydig, F., 1876. Über die allgemeinen Bedeckungen der Amphibien. *Arch. f. mikrosk. Anat.*, **12**: 119-241.

Liem, S. S., 1970. The morphology, systematics and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae). *Fieldiana. Zool.*, **57**: 1-145.

Lorch, P. D., & Eadie, J. M., 1999. Power of the concentrated changes test for correlated evolution. *Syst. Biol.*, **48**. 170-191.

Lynch, J. D., 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Misc. Publ. Mus. nat. Hist. Univ. Kansas*, **53**: 1-238.

Maddison, W., 1990. A method for testing the correlated evolution of two binary characters. Are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution*, **44**: 539-557.

Maddison, W. P. & Maddison, D. R., 1998. – *MacClade. analysis of phylogeny and character evolution version 3.08*. Sunderland, Massachusetts, Sinauer.

Manzano, A., Fabrezi, M. & Vences, M., 2007. Intercalary elements, treefrogs, and the early differentiation of a complex system in the Neobatrachia. *Anat. Rec.*, **290**: 1551-1567.

Mueller, R. L., Macey, J. R., Jaekel, M., Wake, D. B. & Boore, J. L., 2004. - Morphological homoplasy, life history evolution, and historical biogeography of plethodontid salamanders inferred from complete mitochondrial genomes. *Proc. natl. Acad. Sci. USA*, **101**: 13820-13825.

Noble, G. K., 1931. *The biology of the Amphibia*. New York, Dover: i-xviii + 1-577.

Ohler, A. & Dubois, A., 1989. Démonstration de l'origine indépendante des ventouses digitales dans deux lignées phylogenétiques de Ranidae (Amphibiens, Anoures). *C. r. Acad. Sci.*, Paris, **309**: 419-422.

Parker, H. W., 1934. *A monograph of the frogs of the family Microhylidae*. London, British Museum (Natural History): i-viii + 1-208.

Perret, J.-L., 1966. Les amphibiens du Cameroun. *Zool. Jahrb. Syst.*, **93**: 289-464.

Plösch, T., 1991. Die Alizarin /Alcianblau-Färbung nach Dingerkus and Uhler. *Aquar-Terr. Z.*, **44**: 252-254.

Roelants, K. & Bossuyt, F., 2005. Archaeobatrachian paraphyly and Pangaean diversification of crown-group frogs. *Syst. Biol.*, **54**. 111-126.

Roelants, K., Jiang, J. & Bossuyt, F., 2004. – Endemic ranid (Amphibia. Anura) genera in southern mountain ranges of the Indian subcontinent represent ancient frog lineages. evidence from molecular data. *Mol. Phyl. Evol.*, **31**: 730-740.

San Mauro, D., Vences, M., Alcobendas, M., Zardoya, R. & Meyer, A., 2005. Initial diversification of living amphibians predated the breakup of Pangaea. *Amer. Nat.*, **165**: 590-599.

Scotland, R. W., Olmstead, R. G. & Bennett, J. R., 2003. Phylogeny reconstruction. the role of morphology. *Syst. Biol.*, **52**: 539-548.

Scott, E., 2005. – A phylogeny of ranoid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data. *Cladistics*, **21**: 507-574.

Tihen, J. A., 1965. – Evolutionary trends in frogs. *Amer. Zool.*, **5** (2): 309-318.

Van der Meijden, A., Vences, M., Hoegg, S. & Meyer, A., 2005. – A previously unrecognized radiation of ranid frogs in southern Africa revealed by nuclear and mitochondrial DNA sequences. *Mol. Phyl. Evol.*, **37**: 674-685.

Van der Meijden, A., Vences, M. & Meyer, A., 2004. – Novel phylogenetic relationships of the enigmatic brevicipitine and scaphiophrynine toads as revealed by sequences from the nuclear Rag-1 gene. *Proc. r. Soc. Lond.*, (B) (Suppl.), **271**: S378-S381.

Vences, M. & Glaw, F., 2001. – When molecules claim for taxonomic changes: new proposals on the classification of Old World treefrogs. *Spixiana*, **24** (1): 85-92.

Vences, M., Glaw, F., Andreone, F., Jesu, R. & Schimmenti, G., 2002. – Systematic revision of the enigmatic Malagasy broad-headed frogs (*Laurentomantis* Dubois, 1980), and their phylogenetic position within the endemic mantellid radiation of Madagascar. *Contr. Zool.*, **70**: 191-212.

Vences, M., Vieites, D. R., Glaw, F., Brinkmann, H., Kosuch, J., Veith, M. & Meyer, A., 2003. – Multiple overseas dispersal in amphibians. *Proc. r. Soc. Lond.*, (B), **270**: 2435-2442.

Wiens, J. J., 2004. – The role of morphological data in phylogeny reconstruction. *Syst. Biol.*, **53**: 653-661.

Corresponding editor: Annemarie Ohler.

APPENDIX

List of specimens studied. Collection abbreviations are as follows. Museo Regionale di Scienze Naturali, Torino (MRSN), Muséum National d'Histoire Naturelle, Paris (MNHN), Museum of Comparative Zoology, Cambridge (MCZ, housed as exchange in ZSM); Zoölogisch Museum Amsterdam, Amsterdam (ZMA); Zoologische Staatssammlung München, Munchen (ZSM), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Thomas Ziegler working collection (TZ; specimens to be included in ZFMK). Other abbreviations used: SEM, examined by Scanning Electron Microscope, MIC, examined by stereo microscope (and in most cases schematically drawn with the aid of a camera lucida). Character states as used and explained in the text.

Species	Catalogue number	SEM/MIC	Character state
RANOID FAMILIES			
ARTHROLEPTIDAE Mivart, 1869: *ARTHROLEPTINAE* Mivart, 1869			
Arthroleptis adolfifriederici Nieden, 1911	ZFMK 58806	MIC	M
Arthroleptis poecilonotus Peters, 1863	ZFMK 61383, ZFMK 67497	MIC	M
Arthroleptis sp.	ZFMK 68794	MIC	M
Arthroleptis variabilis Matschie, 1893	ZFMK 28960	MIC	M
Arthroleptis [*Schoutedenella*] sp.	MNHN 1979.3852	MIC	H
ARTHROLEPTIDAE Mivart, 1869: *ASTYLOSTERNINAE* Noble, 1927			
Astylosternus montanus Amiet, 1978	ZFMK 67732	MIC	F
Leptodactylodon mertensi Perret, 1959	ZFMK 67746	MIC	A
Scotobleps gabonicus Boulenger, 1900	ZFMK 61330, ZFMK 67755	MIC	Finger: F, toe: hook morphology
Trichobatrachus robustus Boulenger, 1900	ZFMK 68850-68851	SEM, MIC (toe); MIC (finger)	Finger: F, toe: hook morphology
ARTHROLEPTIDAE Mivart, 1869: *LEPTOPELINAE* Laurent, 1972			
Leptopelis bocagii (Günther, 1865)	ZFMK 68787-68788	MIC	A
Leptopelis cf. *mossambicus* Poynton, 1985	ZFMK 29444	MIC	A
Leptopelis modestus (Werner, 1898)	ZFMK 67412	MIC	A
Leptopelis natalensis (Smith, 1849)	ZFMK 68783 (juvenile), 68784, 68786	MIC	A
Leptopelis natalensis (Smith, 1849)	ZFMK 68785	SEM, MIC	A
Leptopelis rufus Reichenow, 1874	ZFMK 67992	MIC	A
BREVICIPITIDAE Bonaparte, 1850			
Breviceps fuscus Hewitt, 1925	ZFMK 68848	MIC	E
Breviceps mossambicus Peters, 1854	ZFMK 68849	SEM, MIC	
CERATOBATRACHIDAE Boulenger, 1884			
Batrachylodes elegans Brown & Parker, 1970	MCZ A 79279 (ZSM 21/1998), MCZ A 79281 (ZSM 23/1998)	MIC	H
Batrachylodes vertebralis Boulenger, 1887	MCZ 44143	MIC	H
Ceratobatrachus guentheri Boulenger, 1884	ZFMK 50483	SEM, MIC	F
Platymantis corrugatus (Duméril, 1853)	ZFMK 63644	SEM, MIC	F
DICROGLOSSIDAE Anderson, 1871			
Euphlyctis ehrenbergii (Peters, 1863)	ZFMK 42842	MIC	F
Fejervarya cancrivora (Gravenhorst, 1829)	ZFMK 20384	SEM, MIC	A or F
Fejervarya limnocharis (Gravenhorst, 1829)	TZ 526; ZFMK 49215	MIC	A or F
Hoplobatrachus chinensis (Osbeck, 1765)	TZ 385	MIC	E
Limnonectes kuhlii (Tschudi, 1838)	TZ 519	MIC	F
Nanorana pleskei Günther, 1896	ZFMK 58098	MIC	I
Occidozyga lima (Gravenhorst, 1829)	ZFMK 68825, ZFMK uncatalogued	MIC	A
Occidozyga martensii (Peters, 1867)	TZ 155	MIC	I
Quasipaa spinosa (David, 1875)	ZFMK 9719	MIC	F
Sphaerotheca breviceps (Schneider, 1799)	ZFMK 13796, ZSM 70/1979	MIC	F
HEMISOTIDAE Cope, 1867			
Hemisus marmoratus (Peters, 1854)	ZFMK uncatalogued ([illegible] specimens)	MIC	I

Species	Catalogue number	SEM/ MIC	Character state
HYPEROLIIDAE Laurent, 1943			
Afrixalus delicatus Pickersgill, 1984	ZFMK 68792	MIC	A
Afrixalus fornasini (Bianconi, 1849)	ZFMK 68789	MIC	A
Afrixalus fulvovittatus (Cope, 1861)	ZFMK 62576	MIC	A
Afrixalus sp	ZFMK uncatalogued	SEM, MIC	A
Afrixalus sp.	ZFMK 68790-68791	MIC	A
Afrixalus sp	ZFMK uncatalogued	MIC	A
Heterixalus alboguttatus (Boulenger, 1882)	ZFMK 68793	MIC	A
Heterixalus andrakata Glaw & Vences, 1991	ZFMK 52561, 52564	MIC	A
Heterixalus betsileo (Grandidier, 1872)	MRSN A.399.4, ZMA 6724, 6756, ZMA FN 995	MIC	A
Heterixalus luteostriatus (Andersson, 1910)	MRSN A.393.7	MIC	A
Heterixalus madagascariensis (Duméril & Bibron, 1841)	ZFMK 52574, 52647	MIC	A
Heterixalus punctatus Glaw & Vences, 1994	ZFMK 60018	MIC	A
Heterixalus rutenbergi (Boettger, 1881)	ZFMK 59844	MIC	A
Heterixalus tricolor (Boettger, 1881)	ZFMK 52583	MIC	A
Heterixalus variabilis (Ahl, 1930)	ZFMK 52578, 53606	MIC	A
Hyperolius argus Peters, 1854	ZFMK 68780	MIC	A
Hyperolius marmoratus Rapp, 1842	ZFMK 68773-68777; ZFMK uncatalogued (2 specimens	MIC	A
Hyperolius nasutus Günther, 1865	ZFMK 68782	MIC	A
Hyperolius pusillus (Cope, 1862)	ZFMK 68781	MIC	A
Hyperolius semidiscus Hewitt, 1927	ZFMK 68779	MIC	A
Hyperolius sp.	ZFMK uncatalogued	MIC	A
Hyperolius tuberilinguis Smith, 1849	ZFMK 68778	MIC	A
Kassina decorata (Angel, 1940)	ZFMK 67841	MIC	H
Phlyctimantis verrucosus (Boulenger, 1912)	ZFMK 58824	MIC	M
Tachycnemis seychellensis (Duméril & Bibron, 1841)	ZFMK 62859, 62879	MIC	M
MANTELLIDAE Laurent, 1946			
Aglyptodactylus madagascariensis (Duméril, 1853)	ZFMK 18954	SEM, MIC	F
Aglyptodactylus madagascariensis (Duméril, 1853)	ZFMK 52682, 60889	MIC	E
Blommersia wittei (Guibé, 1974)	ZFMK 53594	MIC	I
Boophis boehmei Glaw & Vences, 1992	ZFMK 50651	MIC	I
Boophis cf. *madagascariensis* (Peters, 1874)	MRSN	MIC	I
Boophis idae (Steindachner, 1867)	ZFMK 53649	MIC	I
Boophis miniatus (Mocquard, 1902)	ZFMK 48166	MIC	I
Boophis sp. aff. *sibilans*	ZFMK 62797	MIC	I
Boophis tephraeomystax (Duméril, 1853)	ZFMK 68810	SEM	I
Boophis tephraeomystax (Duméril, 1853)	ZFMK 68811	SEM, MIC	I
Gephyromantis webbi (Grandison, 1953)	ZFMK 52726	MIC	I
Guibemantis bicalcaratus (Boettger, 1913)	ZFMK 8877	MIC	I
Guibemantis flavobrunneus (Blommers-Schlösser, 1979)	ZFMK 17621	MIC	I
Laliostoma labrosum (Cope, 1868)	ZMA FN 73; ZFMK 52755, 59965	MIC	F
Laliostoma labrosum (Cope, 1868)	ZFMK 8890, 59967	SEM, MIC	E
Mantella aurantiaca Mocquard, 1900	ZFMK 68807	MIC	I
Mantella crocea Pintak & Bohme, 1990	ZFMK 68806	MIC	I
Mantella madagascariensis (Grandidier, 1872)	ZFMK 68808	MIC	I
Mantidactylus albofrenatus (Müller, 1892)	ZFMK 25373	MIC	I
Mantidactylus grandidieri Mocquard, 1895	MRSN	MIC	I
Mantidactylus ulcerosus (Boettger, 1880)	ZFMK 68805	SEM, MIC	I
Spinomantis aglavei (Methuen & Hewitt, 1913)	ZFMK 46021	MIC	I
MICROHYLIDAE Günther, 1858			
Anodonthyla montana Angel, 1925	MNHN 1972.1112	SEM, MIC	G
Calluella guttulata (Blyth, 1856)	ZFMK 40145	MIC	J
Cophixalus darlingtoni (Loveridge, 1948)	MCZ 71561-71562	MIC	H
Cophixalus riparius Zweifel, 1962	MCZ 70189, 70196	MIC	H
Cophyla phyllodactyla Boettger, 1880	ZFMK 68846	MIC	G
Dermatonotus muelleri (Boettger, 1885)	ZFMK 40975	MIC	F
Gastrophryne cf. *olivacea* (Hallowell, 1856)	ZFMK 68845	SEM, MIC	M
Kaloula pulchra Gray, 1831	ZFMK 6462	MIC	(H, broader)
Microhyla pulchra (Hallowell, 1861)	TZ 530	MIC	F

Species	Catalogue number	SEM MIC	Character state
MICROHYLIDAE Günther, 1858 (continuation)			
Phrynomantis bifasciatus (Smith, 1847)	ZFMK 68843	SEM, MIC	G (tends to J)
Phrynomantis bifasciatus (Smith, 1847)	ZFMK 68844	MIC	G (tends to J)
Phrynomantis microps Peters, 1875	ZFMK 68842	SEM, MIC	G (tends to J)
Scaphiophryne brevis (Boulenger, 1896)	MNHN 1975 2612	SEM, MIC	E
Scaphiophryne calcarata (Mocquard, 1895)	ZFMK 59998	SEM, MIC	F
Scaphiophryne marmorata Boulenger, 1882	ZFMK 50150	MIC	H
PETROPEDETIDAE Noble, 1931			
Petropedetes sp.	MNHN 1989 3999	SEM (3B), MIC	H
PHRYNOBATRACHIDAE Laurent, 1941			
Phrynobatrachus auritus Boulenger, 1900	ZFMK 64261	MIC	G
Phrynobatrachus cf. *versicolor* Ahl, 1924	ZFMK 58788	MIC	H/M
Phrynobatrachus cricogaster Perret, 1957	ZFMK 67299	MIC	H
Phrynobatrachus mababiensis FitzSimons, 1932	ZFMK 68821	SEM (toe IV), MIC	M
Phrynobatrachus mababiensis FitzSimons, 1932	ZFMK 68822	MIC	M
Phrynobatrachus natalensis (Smith, 1849)	ZFMK 68816-68817, 68819-68820	MIC	M
Phrynobatrachus natalensis (Smith, 1849)	ZFMK 68818	SEM (finger III), MIC	M
Phrynobatrachus werneri (Nieden, 1910)	ZFMK 68033	SEM (toe IV), MIC	Finger M (tends to H); toe IV M
Phrynobatrachus cf. *werneri* (Nieden, 1910)	ZFMK 47960, 47992	MIC	H or M
Phrynodon cf. *sandersoni* (Parker, 1935)	ZFMK 67342, 68253, 68257	MIC	H
Phrynodon cf. *sandersoni* (Parker, 1935)	ZFMK 68[illegible]79	SEM MIC	H
PTYCHADENIDAE Dubois, 1987			
Ptychadena bibroni (Hallowell, 1845)	ZFMK 15420	MIC	E
Ptychadena bibroni (Hallowell, 1845)	ZFMK 17017	MIC	Finger E, toe hook morphology
Ptychadena schillukorum (Werner, 1908)	ZFMK 34045	MIC	F
Ptychadena mascareniensis (Duméril & Bibron, 1841)	ZFMK 55157	SEM MIC	Finger F, toe A, tending towards hook morphology
Ptychadena mascareniensis (Duméril & Bibron, 1841)	ZFMK 55621	MIC	E
Ptychadena cf. *mascareniensis* (Duméril & Bibron, 1841)	ZFMK 68826-68827	MIC	E
PYXICEPHALIDAE Bonaparte, 1850			
Cacosternum boettgeri (Boulenger, 1882)	ZFMK 33116	MIC	F
Cacosternum boettgeri (Boulenger, 1882)	ZFMK 33117	SEM, MIC	F
Natalobatrachus bonebergi Hewitt & Methuen, 1912	ZFMK 68812	SEM MIC	H
Natalobatrachus bonebergi Hewitt & Methuen, 1912	ZFMK 68813-68814	MIC	H
Strongylopus grayii (Smith, 1849)	ZFMK 33097	SEM MIC	M
Tomopterna delalandii (Tschudi, 1838)	ZFMK 44598	MIC	F
Tomopterna natalensis (Smith, 1849)	ZFMK 33[illegible]64, 68815	MIC	F
RANIDAE Rafinesque-Schmaltz, 1814			
Hylarana (Amnirana) cf. *albolabris* (Hallowell, 1856)	MNHN 1989.4151	MIC	J
Hylarana (Amnirana) lepus (Andersson, 1903)	ZFMK 64830	MIC	M
Hylarana (Hydrophylax) galamensis (Duméril & Bibron, 1841)	ZFMK 61676	SEM MIC	M
Hylarana (Hylarana) macrodactyla Günther, 1859	TZ 667, ZFMK 43956	MIC	M
Hylarana (Sylvirana) nigrovittata (Blyth, 1856)	TZ 67, 756	MIC	M
Lithobates catesbeianus (Shaw, 1802)	ZFMK uncatalogued (2 juveniles)	MIC	F
Odorrana livida (Blyth, 1856)	TZ 349	MIC	M
Odorrana livida (Blyth, 1856)	TZ 527	SEM, MIC	M
Rana dalmatina Fitzinger in Bonaparte, 1838	ZFMK 68823	MIC	M
Rana temporaria Linnaeus, 1758	ZFMK uncatalogued	MIC	M
Staurois sp.	ZFMK 16597	SEM MIC	I
Staurois sp.	ZFMK 16598	MIC	B
RHACOPHORIDAE Hoffman, 1932			
Chiromantis xerampelina Peters, 1854	ZFMK 39467	MIC	J
Chiromantis xerampelina Peters, 1854	ZFMK 68795	SEM MIC	J
Kurixalus verrucosus (Boulenger, 1893)	TZ 444	MIC	I
Polypedates eques Günther, 1858	ZFMK 68797-68799	MIC	G
Polypedates eques Günther, 1858	ZFMK uncatalogued (5 specimens)	MIC	G

Species	Catalogue number	SEM, MIC	Character state
RHACOPHORIDAE Hoffman, 1932 (continuation)			
Polypedates maculatus (Gray, 1830)	ZFMK 13784-13785	MIC	G
Polypedates otilophus (Boulenger, 1893)	ZFMK 68852	SEM, MIC	G
Rhacophorus dennysi Blanford, 1881	ZFMK 65461	SEM, MIC	G
Rhacophorus nigropalmatus Boulenger, 1895	ZFMK uncatalogued	MIC	G
NON-RANOID FAMILIES			
BOMBINATORIDAE Gray, 1825			
Bombina sp.	ZFMK uncatalogued	MIC	F
CENTROLENIDAE Taylor, 1951			
Hyalinobatrachium fleischmanni (Boettger, 1893)	ZFMK 68768	SEM, MIC	K
DENDROBATIDAE Cope, 1865			
Ameerega silverstonei (Myers & Daly, 1979)	ZFMK 40709, 68828	MIC	H
Colostethus nubicola (Dunn, 1924)	ZFMK 46644	MIC	H
Dendrobates auratus (Girard, 1855)	ZFMK 68837	MIC	H
Dendrobates leucomelas Steindachner, 1864	ZFMK 68839	MIC	H
Dendrobates tinctorius (Cuvier, 1797)	ZFMK 68838	MIC	H
Epipedobates boulengeri (Barbour, 1909)	ZFMK 68829	MIC	H
Oophaga lehmanni (Myers & Daly, 1976)	ZFMK 68834	MIC	H
Oophaga pumilio (Schmidt, 1857)	ZFMK 68836	MIC	H
DISCOGLOSSIDAE Günther, 1858			
Discoglossus cf. *galganoi* Capula, Nascetti, Lanza, Bullini & Crespo, 1985	ZFMK uncatalogued	MIC	E
Discoglossus montalentii Lanza, Nascetti, Capula & Bullini, 1984	ZFMK uncatalogued	MIC	M
Discoglossus sardus Tschudi in Otth, 1837	ZFMK uncatalogued	MIC	M
HELEOPHRYNIDAE Noble, 1931			
Heleophryne regis Hewitt, 1910	ZFMK 68769-68771	MIC	O
HYLIDAE Rafinesque, 1815			
Agalychnis callidryas (Cope, 1862)	ZFMK uncatalogued	SEM, MIC	L
Hyla arborea (Linnaeus, 1758)	ZFMK 68766	MIC	E
Hyla cinerea (Schneider, 1799)	ZFMK uncatalogued	MIC	E
Phyllomedusa sauvagii Boulenger, 1882	ZFMK uncatalogued	MIC	A
MEGOPHRYIDAE Bonaparte, 1850			
Megophrys nasuta (Schlegel, 1858)	ZFMK 68853	MIC	A
MYOBATRACHIDAE Schlegel, 1850			
Limnodynastes sp.	ZFMK uncatalogued	MIC	D
Pseudophryne bibronii Günther, 1859	ZFMK 28[illegible]59	SEM, MIC	E
PIPIDAE Gray, 1825			
Hymenochirus boettgeri (Tornier, 1896)	ZFMK uncatalogued	SEM, MIC	L
Pipa carvalhoi (Miranda-Ribeiro, 1937)	ZFMK uncatalogued	SEM (toe), MIC (finger and toe)	Finger: B, toe: E
Silurana tropicalis Gray, 1864	ZFMK uncatalogued	MIC	N
Xenopus victorianus Ahl, 1924	ZFMK uncatalogued	SEM, MIC	C
CYCLORAMPHIDAE Bonaparte, 1850			
Rhinoderma darwinii Duméril & Bibron, 1841	ZFMK 68767	MIC	M

Alytes, 2009, **26** (1-4): 153-166.

The onomatophores of *Paramesotriton deloustali* (Bourret, 1934) (the seven errors game)

Roger Bour, Annemarie Ohler & Alain Dubois

Reptiles et Amphibiens, UMR 5202 CNRS OSEB,
Département Systématique et Evolution, Muséum national d'Histoire naturelle,
CP 30, 25 rue Cuvier, 75005 Paris, France <bour@mnhn.fr>

In the original description of *Mesotriton deloustali* by René Bourret (1934), no onomatophore (type specimen) was expressly mentioned. However, this description included detailed measurements of two individuals, one of which was pictured on a plate, and a skull was figured on a sketch. These specimens are identified in the MNHN (Muséum national d'Histoire naturelle, Paris), Reptiles and Amphibians collection. A lectophoront (lectotype) is here formally designated, and the two remaining specimens therefore become exonymophoronts (paralectotypes).

INTRODUCTION

Salamanders and newts are amphibians mainly distributed in the northern temperate regions. Few species of Salamandridae Goldfuss, 1820, a Palaearctic family, are known to occur at the northern limit of the Oriental realm. *Paramesotriton deloustali* (Bourret, 1934) is such a species, discovered in the northern part of Vietnam at the beginning of the 20th century but described some decades later. Other members of this genus were known from China, but recently a species was described from Laos (Raffaëlli, 2007). As a result of research on the biography of René Bourret, new data from his notes are available. Thus we restudied his collection and reassessed the status of the specimens of *Mesotriton deloustali* originally from this collection, in particular the onomatophores ("name-bearing types" or "type specimens").

Currently (October 2008), the genus *Paramesotriton* Chang, 1935 includes nine species, *P. chinensis* (Gray, 1859), *P. deloustali* (Bourret, 1934); *P. hongkongensis* (Myers & Leviton, 1962), *P. caudopunctatus* (Liu & Hu, 1973); *P. guangxiensis* (Huang, Tang & Tang, 1983), *P. fuzhongensis* Wen, 1989, *P. laoensis* Stuart & Papenfuss, 2002, *P. zhijinensis* Li, Tian & Gu, 2008, *P. longliensis* Li, Tian, Gu & Xiong, 2008 (Raffaëlli, 2007, Li, Tian & Gu, 2008, Li et al., 2008, Zhao et al., 2008). The affinities of several species, obviously closely related, require to be specified. Moreover, recent work suggests that *P. caudopunctatus* and *P. laoensis* could deserve generic separation (Weisrock et al., 2006, Raffaëlli, 2007). It is also necessary to note nomenclatural problems due to the "double description" of a recent species: the description of *P. zhijinensis* Li, Tian & Gu, 2008 was published in April 2008, i.e., before *P. zhijinensis* Zhao, Che, Zhou, Chen, Zhao & Zhang, 2008, published in May 2008.

Paramesotriton deloustali is known from about ten localities in the following provinces of northern Vietnam: Bac Kan, Ha Giang, Lao Cai, Tay Nguyen, Tuyen Quang, Vinh Phuc and Yen Bai. The population of Lao Cai (north-western Vietnam, west of the Red River), recently discovered in the mounts Hoang Lien (district of Van Ban) could be taxonomically distinct from *Paramesotriton deloustali* (Raffaëlli, 2007 and pers. comm., October 2008). All these uncertainties show that more investigations are needed, especially since most of the species occupy restricted areas and are threatened. Therefore a review of the onomatophores (type specimens) of *Mesotriton deloustali* Bourret, 1934, nucleospecies (type species) of the genus, appears useful.

Methodology

We follow Bourret in designating as Tam Dao the mountain itself (21°31'N, 105°53'N) and its surroundings, in particular the hill station (Bourret, 1940*b*). All studied specimens are deposited in the Reptiles and Amphibians collection of the Muséum national d'Histoire naturelle (MNHN), Paris, France. They were collected by Bourret, who had been forewarned of their existence by "*M. Deloustal*" Eugène Deloustal (1881-1942), friend of René Bourret and chief land surveyor at the Land register and Topographical service at Hanoi, owned a residence at Tam Dao. Actually, according to Catherine Meste (pers. comm., September 2008), grand-daughter of Eugene, the first observation of the salamander in the torrent of the hill station was made by André Deloustal (1909-1996), son of Eugène (fig. 1). We use here the nomenclatural terms defined by Dubois (2005) to designate the various categories of "types" and related expressions.

Nomenclatural status of the specimens of *Mesotriton deloustali* collected by Bourret

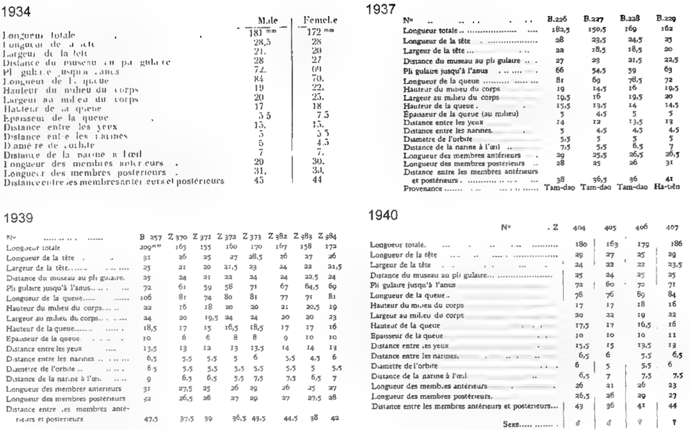
On December 1934, René Bourret described a new genus and a new species of salamander discovered at Tam Dao in Tonkin, then part of French Indo-China. *Mesotriton deloustali* was dedicated to "*M. Deloustal, géomètre au Cadastre*", who had announced its existence to him "*a long time ago*" [depuis longtemps], but the animals had been caught by Bourret himself. The author gave measurements of two individuals (a male 181 mm long, a female of 172 mm), one of them illustrated on a plate; additionally, a skull was outlined (Bourret, 1934) (fig. 2, 3a, 4a). Being the only ones mentioned in the original publication, these three specimens represent the symphoronts (syntypes) of the species. The two measured specimens had been maintained in captivity for one year at the date of description, therefore they had probably been captured in 1933 (see below). Bourret did not precisely mention onomatophores (type specimens), and no registration numbers were given. It was the first

Fig. 1 – Eugène Therèse Louis Deloustal (1881-1942) and his son André Louis Maurice Deloustal (1909-1996), discoverers of *Paramesotriton deloustali* described by BOURRET in 1934. Photographs communicated by Catherine and Michel Meste, their grandsons and nephews.

time that he described an amphibian, as his previous *Notes herpétologiques* were dealing only with snakes. In his personal copy of the original description, Bourret added with pencil 'Z 373' for the individual of 181 mm identified as male and '257' (i.e., B 257) for that of 172 mm identified as female. It is a double error: B 257 is the number that he gave later (1939) to the specimen of 181 mm and Z 373 that which he attributed in the same publication to an unsexed individual captured at Tam Dao in 1938

The following year, Mangven Chang from Shanghai came to work at the Paris Natural History Museum. Studying *Mesotriton deloustali*, beside noticing that the generic nomen *Mesotriton* was nomenclaturally preoccupied, he found that four specimens of this species, accessed in 1908 and 1911, were already in the collection, wrongly identified as *Tylototriton verrucosus* Anderson, 1871 (CHANG, 1935*a*) Shortly after, CHANG (1935*b*) proposed the new genus nomen *Paramesotriton* to replace *Mesotriton* Bourret, 1934, preoccupied by *Mesotriton* Bolkay, 1927 (described as subgenus) a nomen which has *Triton alpestris* Laurenti, 1768 as nucleospecies (type species) by subsequent designation of THORN (1969)

BOURRET mentioned this salamander again, using the nomen *Paramesotriton deloustali*, only in December 1937 He precised that the specimen of 181 mm described in 1934 was still alive, and revealed the capture by himself at Tam Dao, the onymotope (type locality), of 12 new specimens without specifying their sex. The measurements of four of them (B 226 to B 229) were given (tab. 1). In a list of species and a list of specimens, the locality of Ha-Tiên,



1934

	Male	Femele
Longueur totale	181 mm	172 mm
Longueur de la tête	28,5	28
Largeur de la tête	21.	20
Distance du museau au pli gulaire	28	27
Pli gulaire jusqu'à l'anus	72.	69
Longueur de la queue	84	70.
Hauteur du milieu du corps	19	22.
Largeur au milieu du corps	20	25.
Hauteur de la queue	17	18
Epaisseur de la queue	5,5	7,5
Distance entre les yeux	15.	15.
Distance entre les narines	5	5,5
Diamètre de l'orbite	5	4,5
Distance de la narine à l'œil	7	7.
Longueur des membres antérieurs	29	30.
Longueur des membres postérieurs	31.	30.
Distance entre les membres antérieurs et postérieurs	45	44

1937

Nº	B.226	B.227	B.228	B.229
Longueur totale	182,5	150,5	169	162
Longueur de la tête	28	23,5	24,5	25
Largeur de la tête	22	18,5	18,5	20
Distance du museau au pli gulaire	27	23	21,5	22,5
Pli gulaire jusqu'à l'anus	66	54,5	59	63
Longueur de la queue	81	69	78,5	72
Hauteur du milieu du corps	19	14,5	16	19,5
Largeur au milieu du corps	19,5	16	19,5	20
Hauteur de la queue	15,5	13,5	14	14,5
Épaisseur de la queue (au milieu)	5	4,5	5	5
Distance entre les yeux	14	12	13,5	13
Distance entre les narines	5	4,5	4,5	4,5
Diamètre de l'orbite	5,5	5	5	5
Distance de la narine à l'œil	7,5	5,5	6,5	7
Longueur des membres antérieurs	29	25,5	26,5	26,5
Longueur des membres postérieurs	28	25	26	31
Distance entre les membres antérieurs et postérieurs	38	36,5	36	41
Provenance	Tam-dao	Tam-dao	Tam-dao	Ha-tiên

1939

Nº	B 257	Z 370	Z 371	Z 372	Z 373	Z 382	Z 383	Z 384
Longueur totale	209 mm	165	155	160	170	167	158	172
Longueur de la tête	31	26	25	27	28,5	26	27	26
Largeur de la tête	25	21	20	21,5	23	24	22	21,5
Distance du museau au pli gulaire	25	24	21	22	24	24	22,5	24
Pli gulaire jusqu'à l'anus	72	61	59	58	71	67	64,5	69
Longueur de la queue	106	81	74	80	81	77	71	81
Hauteur du milieu du corps	22	16	18	20	20	21	20,5	19
Largeur au milieu du corps	24	20	19,5	24	24	20	20	23
Hauteur de la queue	18,5	17	15	16,5	18,5	17	17	16
Epaisseur de la queue	10	6	6	8	8	9	10	10
Distance entre les yeux	13,5	13	12	13	13,5	14	14	13
Distance entre les narines	6,5	5,5	5,5	5	6	5,5	4,5	6
Diamètre de l'orbite	6,5	5,5	5,5	5,5	5,5	5,5	5	5,5
Distance de la narine à l'œil	9	6,5	6,5	5,5	7,5	7,5	6,5	7
Longueur des membres antérieurs	31	27,5	25	26	29	26	25	27
Longueur des membres postérieurs	32	26,5	26	27	29	27	27,5	28
Distance entre les membres antérieurs et postérieurs	47,5	37,5	39	36,5	43,5	44,5	38	42

1940

Nº . Z	404	405	406	407
Longueur totale	180	163	179	186
Longueur de la tête	29	27	25	29
Largeur de la tête	24	22	22	23,5
Distance du museau au pli gulaire	25	24	25	25
Pli gulaire jusqu'à l'anus	72	60	72	71
Longueur de la queue	78	76	89	84
Hauteur du milieu du corps	17	17	18	16
Largeur au milieu du corps	20	22	19	22
Hauteur de la queue	17,5	17	16,5	16
Epaisseur de la queue	10	10	10	11
Distance entre les yeux	15,5	15	13,5	13
Distance entre les narines	6,5	6	5,5	6,5
Diamètre de l'orbite	6	5	5,5	6
Distance de la narine à l'œil	6,5	7	7,5	7,5
Longueur des membres antérieurs	26	21	26	23
Longueur des membres postérieurs	26,5	26	29	27
Distance entre les membres antérieurs et postérieurs	43	36	41	44
Sexe	♂	♂	♀	?

Fig. 2. Measurements of *Paramesotriton deloustali* (Bourret, 1934) taken by Bourret, such as they were published by himself (BOURRET, 1934, 1937, 1939, 1940*a*). Tables reproduced as facsimile

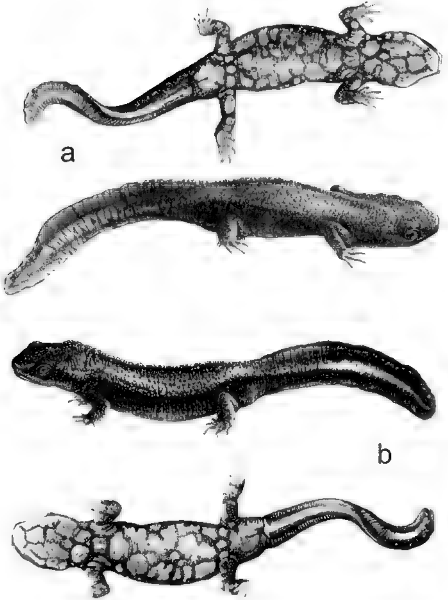


Fig. 3. — *Paramesotriton deloustali* (Bourret, 1934), male specimen MNHN 1935.119, lectophoront (lectotype) of the species. (a) From BOURRET (1934: plate). (b) Water colour (original) by Nguyên-Van-Xuân, reproduced in BOURRET (1942).

Table 1. Main measurements (in millimetres) of the lectophoront (lectotype), MNHN 1935.119, and of one of the two exonymophoronts (paralectotypes), MNHN 1948.110, of *Paramesotriton deloustali* (Bourret, 1934). Comparison with the figures given by Bourret in his publications (see fig. 2). The methods used to take these measurements (landmarks) are obviously distinct for the limbs.

Reference or registration number	Lectophoront (lectotype) MNHN 1935.119		Exonymophoront (paralectotype) MNHN 1948.110	
Source of measurements	Bourret, 1934	Our measurements	Bourret, 1939 (B.257)	Our measurements
Sex	'♀'	♂	♀	♀
Total length	172	170	209	208
Snout-vent length		84.5	97 (25 + 72)	100
Head width	20	20.8	25	25.0
Distance snout – gular fold	27	26.5	25	23.5
Tail length	70	72.2	106	100
Maximum tail heigth	18	18.0	18.5	17.8
Distance between eyes	15	12.5 – 15.0	13.5	13.0 – 16.0
Minimum distance between nostrils	5.5	5.5	6.5	6.0
Maximum diameter of orbit	4.5	4.4	6.5	6.3
Minimum distance nostril eye	7	6.5	9	7.8
Forelimb length	30	27	31	29
Hindlimb length	30	26	32	28
Distance between forelimb and hindlimb	44 (?)	37.5	47.5	48

in Cochinchina, was twice erroneously associated with the specimen B.229 (Bourret, 1937). In this note, for the first time Bourret gave the registration numbers of his collection of amphibians. B.1 was attributed to a specimen of *Rana tigrina rugulosa* Wiegmann, 1834, a junior synonym of *Hoplobatrachus chinensis* (Osbeck, 1765). It is surprising that Bourret did not number all the twelve collected individuals of *Paramesotriton*. Pure assumption, one could think that the four specimens B.226-B.229 were already present in the collection in 1934, so that they would belong, if not in the onomatophores, at least in the hypodigm, material seen by the author at the time of the first description of the taxon (Simpson, 1940). Later, Bourret himself (1942, see below) considered two of them (B.226 and B.228) as belonging to the symphoronts. This interpretation, hardly plausible, is anyway not necessary for the knowledge of the species.

As soon as February 5th, 1935, the Paris Natural History Museum had received a sending from Bourret, including a specimen in alcohol (recorded under number MNHN 1935.119) and a skull (MNHN 1935.120) of his new species of salamander, as well as a turtle. THIREAU (1986) rightly noted that the skull could be that illustrated by BOURRET (1934), so that it would be the third original symphoront. A careful study of this skull reveals that it is unquestionably the very one depicted by BOURRET A noticeable dissymmetry at the level of the anterior half of the vomers and of the ventral opening of the choanae is accurately depicted on the sketch (fig. 4b). On the other hand, the specimen MNHN 1935.119 is clearly that which had been illustrated on the plate included in the original description: the colour pattern of the ventral face, very variable in this species and allowing individual recognition of specimens, is identical (fig. 5) This specimen is a member of the symphoronts, a male, with a length of 170 mm (tab. 1). An error appears in connection with the data given by BOURRET about this salamander. in the original description, the author specified "*One of them* [specimens measured and alive] *is illustrated in natural size on the opposite plate*". However, the male measured 181 mm in 1934 It is difficult to admit that it lost approximately 10 mm length, especially as BOURRET announced it as being still alive in 1937 Consequently, we question the identity of the second measured specimen, the "female" of 172 mm. The overall length of the specimen and several measurements, as well as dimensions of the illustrated salamander, correspond rather well to those given by BOURRET We must thus admit that the "female" of 172 mm of the original description is the specimen MNHN 1935.119, a male. One can be astonished that Bourret has sacrificed a living individual, kept in captivity for one year, to give it to the Paris Museum. Most probably he did not have any other specimen at hand at that time. This specimen still carries a label, "Tamdao 1934", which would be in contradiction with a capture in 1933. However, this label is not original, as the salamander had been kept alive for one year

In February 1939, BOURRET gave measurements of eight specimens, all passed away during the summer of 1938: the specimen kept alive since 1933 (or 1934), already mentioned in 1937, numbered B.257, and seven others captured at Tam Dao in 1938, numbered Z 370 to Z.373 and Z.382 to Z.384 (BOURRET, 1939*a*) (fig. 2). Another mistake, partly corrected by BOURRET, appeared in this note· the B 257 specimen was identified as a female (of 209 mm), whereas the previous note (1937) mentioned the specimen of 181 mm, the male of the original description, as being the specimen kept alive. Obviously, there already had been a confusion made by Bourret in the identification of the sex. He probably had made an inversion. we can conclude that the specimen of 181 mm (in 1934) and of 209 mm (in 1939), *a posteriori* numbered B 257 and finally identified as a female, is the second symphoront measured by the author.

During the year 1939, Bourret captured four new adult specimens, again at Tam Dao, measured and numbered Z 404 to Z.407. The sex of one of them was not established, indicating the difficult sexing of this species (BOURRET, 1940*a*) (fig 2) In the following two notes, the author repeated that *Paramesotriton deloustali* was known only from Tam Dao (BOURRET, 1940*b-c*).

Finally, in his monograph *Les Batraciens de l'Indochine*, BOURRET (1942) proposed new description and illustrations of the salamander. Unfortunately, two new errors appeared in this work. The illustration inserted in the text shows, according to the caption, the specimen B 226, this caption indicates that this same specimen is also represented on colour plate I,

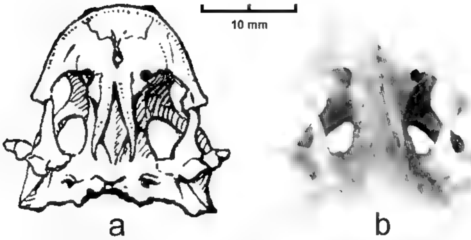


Fig. 4. *Paramesotriton deloustali* (Bourret, 1934). (a) Sketch of the skull published by Bourret (1934) in the original description, exonymophoront (paralectotype) of the species. (b) Skull MNHN 1935.120, exonymophoront (paralectotype) of the species, condylo-basal length: 19.2 mm. Both in ventral view.

figure A. But this plate depicts the specimen already illustrated in 1934, i.e., that given to the Paris Museum, MNHN 1935.109. Amazingly, these two illustrations (1934 and 1942), although unquestionably based on the same individual, are significantly different (fig. 3). The engraving in black and white (1934) was probably obtained starting from a photograph, whereas the figure of the plate (1942) was the reproduction of a water colour suggesting that the specimen was alive. The original of this figure, made by Nguyen-Văn-Xuân, was given by Bourret to the MNHN in 1947, together with all the illustrations of his monograph. Another mistake was of nomenclatural order: Bourret indicated that "*the types are preserved at the Laboratory of the Natural Science at the Indochinese University under the numbers 226, 228, 257 and* [skull] *287*". However, the specimens B.226 and B.228 were first mentioned only in 1937 and they almost surely do not form part of the onomatophores of the original description (see above). On the other hand, the specimen B.257 is one of the two measured symphoronts, the second one being that recorded under number MNHN 1935.119. Lastly, the skull MNHN 1935.120 being, as shown above, the very specimen illustrated in the original description and therefore the third symphoront, the skull B.287 cannot have this status.

In a letter dated June 22nd, 1946 addressed to his mentor, the geologist Charles Jacob, Bourret wrote "*I do not know when I will be able to recover the whole* [personal copies of his publications, personal library], *as well as some specimens in the collections which I intended to keep for the Natural History Museum of Paris (in particular types of new species). I would not like to leave before this question is settled*" (Archives of the Institute of France, Jacob collection). Bourret managed to leave Indo-China the following year, whereas another boat brought his works back to France. The onomatophores were actually given to the Paris Museum. For his *Paramesotriton deloustali*, Bourret gave the specimens B.257, B.226 and B.229, that were renumbered respectively MNHN 1948.110, 111 and 109 (fig. 6-7). The B.257

Fig. 5. *Paramesotriton deloustali* (Bourret, 1934). Male specimen MNHN 1935.119, lectophoront (lectotype); present state, dorsal and ventral view.

specimen is that which had lived 5 years in captivity, the female of 181 mm which had reached 209 mm, symphoront of the species (tab. 1). On the other hand, similar to B.226 already mentioned, B.229 cannot belong to the onomatophores. Moreover, during recording in the catalogue of the Paris Museum, it had been erroneously associated with the locality Ha-Tiên, a mistake probably originating from BOURRET's (1937) note (see above). In addition, and it is there an extra error, as opposed to what indicates the caption of the figure published in 1942, the specimen shown is quite distinct from that labelled B.226 when it was given to the Paris

Fig. 6. *Paramesotriton deloustali* (Bourret, 1934). Female MNHN 1948.110 (ex B.257), exonymophoront (paralectotype); present state, dorsal and ventral view.

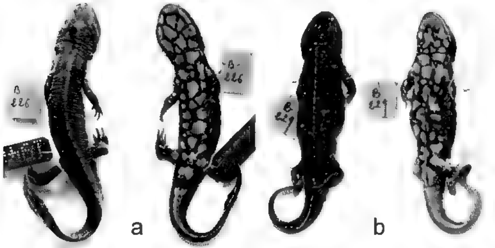


Fig. 7. *Paramesotriton deloustali* (Bourret, 1934). Other specimens given by René Bourret to the Museum of Natural History, Paris: male MNHN 1948.111 (ex B.226); male MNHN 1948.109 (ex B.229). Both in dorsal and ventral view.

Museum (MNHN 1948.111). Either there was confusion in the caption, or the specimen given to the MNHN was not B 226. The second alternative is less probable, the attached tag being handwritten by Bourret himself. The complete list of the specimens of *Paramesotriton deloustali* (Bourret, 1934) measured by Bourret is presented in fig. 2. Table 2 summarises the history of the various specimens of Bourret and their designations in his publications.

CONCLUSION

It is obvious that the absence of registration numbers and of formal designation of nomen-bearing types, as well as an inversion of the sex determination in the original description of *Mesotriton deloustali* by BOURRET, were sources of confusions which made the precise identification of the symphoronts of the species difficult. The male specimen MNHN 1935.119 and the female specimen MNHN 1948.110 are unquestionably those whose measurements are given in the original description of the species in 1934: they are two certain symphoronts. The skull MNHN 1935.120, illustrated in the original description, is the third symphoront. Only the first of them had until now been recognized as "type". CHANG (1935*a*) considered it as a "cotype" (syntype). GUIBÉ (1950) mentioned it as a "paratype", without however specifying the identity of the holotype, giving a length of 198 mm (error for 168 mm?). THIREAU (1986) recognized it as "syntype", but, probably following BOURRET, identified it as a female and gave a length of 172 mm. THIREAU put the specimens MNHN 1935.120 (skull), MNHN 1948.110 (B.257) and MNHN 1948.111 (B.226) in the category "materials

Table 2. Summary of history of specimens of *Paramesotriton deloustali* (Bourret, 1934) mentioned by BOURRET in his works of 1934, 1937, 1939, 1940 and 1942. Data between quotation marks are in error

Specimen	Status	MNHN	1934	1937	1939	1940	1942 text	1942 figure
Male	Lectophoront	1935.119	"Femelle"					"B 226"
Female	Exonymophoront	1948.110	"Mâle"		B.257		B.257	B.257
Skull	Exonymophoront	1935.120	Crâne					
B.226	Aphoront	1948.111		B.226			B.226	
B.227	Aphoront			B.227				
B.228	Aphoront			B.228			B.228	
B.229	Aphoront	1948.109		B.229				
Z.370	Aphoront				Z.370			
Z.371	Aphoront				Z.371			
Z.372	Aphoront				Z.372			
Z.373	Aphoront				Z.373			
Z.382	Aphoront				Z.382			
Z.383	Aphoront				Z.383			
Z.384	Aphoront				Z.384			
Z.404	Aphoront					Z.404		
Z.405	Aphoront					Z.405		
Z.406	Aphoront					Z.406		
Z.407	Aphoront					Z.407		
B.285	Aphoront							B.285 (Skull)
B.287	Aphoront						B.287 (Skull)	

under justice" (they "*require a very thorough specific study*"). The status of MNHN 1948.109 (B.229, "Ha-Tiên") was not specified by THIREAU.

We formally designate here the male specimen registered as MNHN 1935.119 as the lectophoront (lectotype) of *Mesotriton deloustali* Bourret, 1934. It is the specimen illustrated twice in the publications of the author (fig. 3), and thus the best known among the scientific community. This designation is therefore in agreement with the recommendation 74B of the *International Code of Zoological Nomenclature* (ANONYMOUS, 1999): "*an author who indicates a lectotype should give the preference to a syntype whose illustration was published*". Consequently, the specimen MNHN 1948.110 (B.257) is one of the two exonymophoronts (paralectotypes) of the species. The second exonymophoront is the specimen whose skull was drawn by BOURRET in 1934. It is recorded in the Paris Museum under the number MNHN 1935.120. The precise onymotope (type locality) is the torrent of the hill station of Tam Dao (Tam Đảo), province of Vĩnh Phúc, Vietnam (at an altitude of approximately 900 meters according to BOURRET, 1940*b*). Nowadays, according to Thomas Schöttler (pers. com. to RAFFAËLLI, 2007), the adults seem to have disappeared from the pool located downstream from the brook at Tam Dao.

ACKNOWLEDGMENTS

We thank Jean Raffaëlli for his communications and his review of the manuscript, Florence Greffe, curator, and Claudine Pouret, librarian, "Archives et Patrimoine historique" section of the Institute of France (Academy of Sciences), for their warm welcome, Catherine and Michel Meste, who kindly provided data and portraits of their grand-father and uncle Eugene and André Deloustal respectively.

LITERATURE CITED

ANONYMOUS, 1999. *International Code of Zoological Nomenclature*. 4th Edition. London, ICZN: i-xxix + 1-306.

BOURRET, R., 1934. Notes herpetologiques sur l'Indochine française. VII. Une salamandre nouvelle vivant au Tonkin. *Bulletin général de l'Instruction publique*, **14** (1934-1935), (4) (Décembre), 83-84 [11-12], 1 pl.

----- 1937. Notes herpétologiques sur l'Indochine française. XIV. Les Batraciens de la Collection du Laboratoire des Sciences Naturelles de l'Universite. Descriptions de quinze especes ou varietes nouvelles. *Bulletin général de l'Instruction publique*, **17** (1937-1938), (4) (Decembre), *Annexe*: 5-56.

----- 1939. Notes herpetologiques sur l'Indochine française. XVII. Reptiles et Batraciens reçus au Laboratoire des Sciences naturelles de l'Université au cours de l'annee 1938. *Bulletin general de l'Instruction publique*, **18** (1938-1939), (6) (Fevrier), *Annexe*: 13-34, 1 pl.

----- 1940*a*. Notes herpétologiques sur l'Indochine française. XVIII. Reptiles et Batraciens reçus au Laboratoire des Sciences Naturelles de l'Universite au cours de l'annee 1939. Descriptions de quatre espèces et d'une variété nouvelles. *Bulletin général de l'Instruction publique*, **18** (1938-1939), (4) (Décembre 1939), *Annexe*: 5-39, 1 pl.

1940*b*. Notes herpétologiques sur l'Indochine française. XIX. La faune herpetologique des stations d'altitude du Tonkin. *Bulletin general de l'Instruction publique*, **18** (1938-1939), (4) (Décembre 1939), *Annexe*: 41-47.

----- 1940*c*. Notes herpetologiques sur l'Indochine française. XX. Liste des Reptiles et Batraciens actuellement connus en Indochine Française. *Bulletin général de l'Instruction publique*, **18** (1938-1939), (4) (Décembre 1939), *Annexe*: 49-60.

----- 1942. *Les Batraciens de l'Indochine*. Hanoi, Institut Oceanographique de l'Indochine, 6e memoire: i-x + 1-517, pl. 1-4.

CHANG, M. L. Y., 1935*a*. Note relative au Batracien urodèle *Mesotriton deloustali* Bourret. *Bulletin du Muséum d'Histoire Naturelle*, (2), **7** (2) [41]: 95-98.

----- 1935*b*. Note preliminaire sur la classification des Salamandres d'Asie orientale. *Bulletin de la Société zoologique de France*, **60**: 424-427.

DUBOIS, A., 2005. Proposed Rules for the incorporation of nomina of higher-ranked zoological taxa in the *International Code of Zoological Nomenclature*. 1. Some general questions, concepts and terms of biological nomenclature. *Zoosystema*, **27** (2): 365-426.

GUIBÉ, J., 1950. *Catalogue des types d'Amphibiens du Muséum national d'Histoire naturelle*. Paris, Imprimerie nationale: 1-71.

LI, S., TIAN, Y.-Z. & GU, X.-M. 2008 [April]. A new species of the genus *Paramesotriton* (Caudata, Salamandridae). *Acta zootaxonomica sinica*, **33**: 410-413.

Li, S., Tian, Y.-Z., Gu, X.-M. & Xiong, R.-C., 2008 [22 June]. A new species of *Paramesotriton* – *Paramesotriton longliensis* (Caudata: Salamandridae). *Zoological Research*, Kunming, **29** (3): 313-317.

Raffaëlli, J., 2007. *Les Urodeles du monde*. Plumelec, Penclen edition: [i-vi] + 1-377.

Simpson, G. G., 1940. Types in modern taxonomy. *American Journal of Science*, **238**: 413-431.

Thireau, M., 1986. *Catalogue des types d'Urodeles du Museum national d'Histoire naturelle*. Paris, MNHN, Laboratoire de Zoologie (Reptiles et Amphibiens): 1-96.

Thorn, R., 1969. *Les Salamandres d'Europe, d'Asie et d'Afrique du Nord*. Paris, Paul Lechevalier, "1968": i-iv + 5-376.

Weisrock, D. W., Papenfuss, T. J., Macey, J. R., Litvinchuk, S. N., Polymeni, R., Ugurtas, I. H., Zhao, E., Jowkar, H. & Larson, A., 2006. A molecular assessment of phylogenetic relationships and lineage accumulation rates within the family Salamandridae (Amphibia, Caudata). *Molecular Phylogenetics and Evolution*, **41**: 368-383.

Zhao, H., Che, J., Zhou, W., Chen, Y., Zhao, H. & Zhang, Y.-P., 2008 [23 May]. A new species of *Paramesotriton* (Caudata: Salamandridae) from Guizhou Province, China. *Zootaxa*, **1775**: 51-60.

Corresponding editors: Franco Andreone & Masafumi Matsui.

Alytes, 2009, **26** (1-4): 167-175.

Miscellanea nomenclatorica batrachologica

20. Class-series nomina are nouns in the nominative plural: Terrarana Hedges, Duellman & Heinicke, 2008 must be emended

Alain Dubois

Reptiles & Amphibiens, UMR 5202 CNRS OSEB,
Departement Systématique & Evolution, Museum National d'Histoire Naturelle,
CP 30, 25 rue Cuvier, 75005 Paris, France
<adubois@mnhn.fr>

Although their nomenclature is currently not governed by the *Code*, class-series nomina in zoology have always been nouns in the nominative plural, and this should become a formal Rule of the *Code*. About 600 nomina have been created since 1758 for taxa above the rank superfamily in the class Amphibia, and they all followed this universal "implicit Rule". An exception is the recently published nomen Terrarana Hedges, Duellman & Heinicke, 2008, which is a noun in the nominative singular. Two possible emendations are here proposed for this nomen. As for many other nomina of higher taxa, the spelling that will be retained by the majority of authors will become the correct one. This paper also discusses briefly the problems created by the premature creation of class-series nomina, mostly based on quantitative criteria such as a high number of included species, in a group like the amphibians, whose phylogeny and taxonomy are still under frequent and important changes and not yet stabilized.

Typographical conventions. — In the text below, species-series and genus-series nomina (see Dubois, 2000) are printed, as usual, in lower case *italics*, whereas nomina of higher-ranked taxa are written in small capitals, family-series nomina are in *italics*, and class-series nomina in **bold**. Nomenclaturally unavailable nomina (anoplonyms) (see Dubois, 2000) are presented "between quotation marks". Vernacular nomina, i.e. nomina that are not Latin or latinized, are presented underlined. "The *Code*" refers to the fourth edition, currently in force, of the *International Code of Zoological Nomenclature* (Anonymous, 1999), which is here quoted as "Anonymous" for reasons explained in Dubois (2008*b*).

CLASS-SERIES NOMINA ARE NOUNS IN THE NOMINATIVE PLURAL

In order to communicate efficiently about organisms, biologists and non-biologists need a system of classification of the latter into taxa (taxonomy) and of nomination of taxa (nomenclature). Scientific nomina are not definitions of taxa, evolutionary or other theories, or praises for persons, but just neutral, meaningless labels pointing unambiguously and universally to taxa as defined within the frame of given taxonomies (Dubois & Raffaëlli, 2009). To be able to play this role, biological nomenclature must follow a set of Rules, provided in zoology by the *Code*.

The current *Code* regulates the nomenclature of zoological taxa in three "groups of names" or *nominal-series* (Dubois, 2000): the *species-*, *genus-* and *family-series*. Except for a few general statements (Art. 1-4, 7-10, 11.1-11.3, 14, 27-28 and 32.5.2.6), it does not provide binding Rules for the nomenclature of higher taxa (above the rank superfamily), i.e., for *class-series* nomina. This is a potential source of confusion and miscommunication between scientists. It is particularly problematic at a time when, as a result of the various phylogenetic analyses that are regularly produced, numerous such taxa are recognized and named. To avoid the progressive development of a "nomenclatural chaos" in higher taxonomy, Dubois (2005*a-b*, 2005*e*, 2006*a-b*, 2007*a*) proposed a set of Rules to govern this nomenclature.

In the three nominal-series covered by its Rules, the *Code* states what kinds of nomina are acceptable. Thus, a family-series nomen must be "*a noun in the nominative plural*" based on an available generic nomen (Art. 11.7), a genus-series nomen "*must be a word of two or more letters and must be, or be treated as, a noun in the nominative singular*" (Art. 11.8) and a species-series nomen must be "*a word of two or more letters, or a compound word*", and be, or be treated as, either an adjective or a participle in the nominative singular agreeing in grammatical gender with the generic nomen, a noun in the nominative singular standing in apposition to the generic nomen, or a noun or an adjective in the genitive case (Art. 11.9). These possibilities are limited: for example, a genus-nomen cannot be an adjective (but see Dubois, 2007*b*), and a specific epithet cannot be a verb, an adverb, or a noun or an adjective at a case other than nominative or genitive.

In contrast, the *Code* does not provide any Rule or recommendation for the formation of the nomina of higher taxa. However, it has been a universal practice since Linnaeus (1758) to use, for such taxa, nouns in the nominative plural, or treated as such, just like in the family-series. The logic behind this is simple: lower ranked nomina (species, genera) are in the singular, and higher ranked nomina (tribes, families and above) are in the plural. In class-series nomina, the plural is easy to recognize for terms that were borrowed without change from classical Latin. This was often the case in early zoology, as can be exemplified by looking at some of the class-series nomina in Linnaeus (1758) (see Dubois, 2007*d*). Thus, his nomen **Ferae** is the nominative plural of *fera* ("wild animal"), his **Cete** that of Plinius' Latin noun *cetos* ("large sea animal, whale") and his **Aves** that of the Latin noun *avis* ("bird"). It is sometimes less straightforward to ascertain the etymology of nomina that were not borrowed directly from classical Latin nouns, but based on terms from other languages including Greek, or from neologisms derived from combined Latin, including lower Latin, roots.

The nomina not directly borrowed from classical Latin are the overwhelming majority of class-series nomina in zoology. Regarding these nomina, given the possibilities offered by the Latin grammar, which are not unlimited (see e.g. Dubois, 2007*b*), it is usually rather easy to assume the nominative singular from which they were derived. Thus, many nomina ending in "-a" can be assumed to be derived from "neo-Latin" neuter nouns of the second declension, with nominative singulars in "*-um*" (or rarely in "*us*", e.g., *virus*), but there are other possibilities (neuter nouns of the third and fourth declensions, with various endings in the nominative singular). Similarly, nomina ending in "-i" must be assumed to be derived from masculine or feminine nouns of the second declension (nominative singular in "*-us*" or "*-er*"), those ending in "-ae" from feminine or masculine nouns of the first declension (nominative singular usually in "*-a*", with a few exceptions in "*-as*" or "*-es*"), those ending in "-es" from masculine or feminine nouns of the third or fifth declensions (various kinds of nominative singulars), those in "-us" from masculine or feminine nouns of the fourth declension (nominative singular in "*-us*"), and the very rare ones in "-e" from neuter nouns of the second declension (e.g., *cetos* in Plinius). Despite the variability mentioned above, it should be noted that, if class-series nomina are to be Latin or latinized nouns in the nominative plural, only six endings ("-a", "-ae", "-es", "-i", "-us" and exceptionally "-e") are acceptable for them, whereas other endings (e.g., "-as", "-is", "-on", "-os" or "-um") are not.

These "implicit Rules" of formation of class-series nomina have been followed until now by virtually all authors. This is the case for example for all class-series nomina created from 1758 to 2007 for animal taxa currently placed in the class **Amphibia**, which are about 600 in number. Partial reviews of these nomina are to be found in Kuhn (1967), Dubois (1984, 2004*a*, 2005*c-d*), Frost et al. (2006) and Grant et al. (2006), and a complete review will soon be available (Dubois & Frétey, in preparation). These nomina include: (1) nomina in the nominative plural directly borrowed from Latin language (e.g., **Caudata** Scopoli, 1777; **Nuda** Oppel, 1811, **Pedata** Fischer, 1808, **Sirenes** Gray, 1825; **Tritones** Gray, 1850); (2) nomina in the nominative plural ending in "-a", assumed to be derived from "neo-Latin" neuter nouns of the second declension, or possibly from neuter nouns of the third and fourth declensions, with various endings in the nominative singular (e.g., **Amphipneusta** Merrem, 1820; **Dipnoa** Leuckart, 1821, **Gymnophia** Rafinesque-Schmaltz, 1814, **Neobatrachia** Reig, 1958; **Salientia** Laurenti, 1768); (3) nomina in the nominative plural ending in "-i", assumed to be derived from "neo-Latin" masculine or feminine nouns of the second declension (e.g., **Acerci** Wagler, 1828, **Caudati** Duméril, 1806; **Geophili** Fitzinger, 1843, **Lacertini** Gray, 1850, **Neobatrachii** Sarasin & Sarasin, 1890); (4) nomina in the nominative plural ending in "-ae", assumed to be derived from "neo-Latin" masculine or feminine nouns of the first declension (e.g., **Aglossae** Wagler, 1830, **Calamitae** Link, 1807, **Cryptopleurae** Fitzinger, 1843; **Geomolgae** Ritgen, 1828, **Pseudosalamandrae** Bonaparte, 1850), (5) nomina in the nominative plural ending in "-es", assumed to be derived from "neo-Latin" masculine or feminine nouns of the third or fifth declension (e.g., **Batrachophides** Latreille, 1825; **Bufoniformes** Cope, 1864; **Helminthophes** Wagler, 1824, **Meantes** Linnaeus, 1767; **Scolecodes** Ritgen, 1828). All these 600 or so nomina are therefore nouns in the nominative plural, including all the class-series nomina coined in the two recent works of Frost et al. (2006) and Grant et al. (2006). So these "implicit rules" could have been considered shared by all taxonomists, even in the absence of a written statement in this respect in the *Code*.

THE NEED OF AN EMENDATION FOR **TERRARANA**

This is not true, as shown be the recent erection by HEGDES et al. (2008), in a well-known international refereed journal, of a new class-series taxon of **AMPHIBIA** which they called **TERRARANA**, a nomen which is clearly a noun in the nominative singular, as stated expressly by HEDGES et al. (2008: 21) "The name is derived from the Latin, *terra* (land) and *rana* (frog)". For this nomen to be considered a noun in the nominative plural, it should have been derived from a neuter noun ending in "-*um*" in the nominative singular, thus "*Terraranum*", which is clearly not the etymology indicated by the authors. The correct nominative plural for **TERRARANA** would be "**TERRARANAE**".

Beside being in the nominative singular, the nomen **TERRARANA** is also ill-chosen for being formed exactly in the same manner as many genus-series nomina of **AMPHIBIA** that were built by adding a short root (usually of two syllables) before the generic nomen *Rana* Linnaeus, 1758 e.g., *Hylarana* Tschudi, 1838, *Nanorana* Günther, 1896 or *Chaparana* Bourret, 1939. Most of these nomina were created to designate taxa (genera or subgenera) of the family *RANIDAE* Rafinesque-Schmaltz, 1814 and related groups (DUBOIS, 1992; FROST et al., 2006), but some also exist in other amphibian groups, e.g., *Silurana* Gray, 1865, *Cyclorana* Steindachner, 1867 or *Rupirana* Heyer, 1999 (see FROST et al., 2006). For all amphibian taxonomists, the nomen **TERRARANA** will therefore evoke a genus, not a higher taxon. Besides, the spelling "*Terrarana*" not being preoccupied in the genus-series, it could validly be used in any zoological group to name a genus or a subgenus. Such cases of "hemihomonymy" (STAROBOGATOV, 1991), e.g., between the generic nomen *Ranoidea* Tschudi, 1838 and the superfamilial nomen *RANOIDEA* Rafinesque-Schmaltz, 1814, should preferably be avoided, as they are likely to cause confusions, in particular for candid users of electronic databases looking for zoological nomina (HILLIS, 2006, DUBOIS, 2007*c*). These statements are conform to the Recommendation 5 of Appendix B of the *Code*, which reads: "*New names (...) should not be liable to confusion with those of other taxa of any rank (...)*."

Currently, class-series nomina not being covered by the *Code*, any author is entitled to use "his/her own nomenclature" for such nomina, without caring for priority or other criteria, and this is indeed what is being done in many cases (DUBOIS, 2004*a*; DUBOIS & OHLER, 2009). The only existing complete set of Rules for such nomina is that proposed by DUBOIS (2005*a*,*e*, 2006*a*). In fact, these Rules allow here to solve the two nomenclatural problems posed by the creation of the nomen **TERRARANA**.

According to the Rules (R8), (R21) and (R22) of DUBOIS (2006*a*: 229, 232), a class-series nomen may have received various spellings in its history, including its original one (*protonym*) and subsequent ones (*aponyms*). The term aponym is clearer than the ambiguous one of "emendation", which can designate either a change in spelling of the nomen, in its rank or onymorph (hence a nomenclatural concept), or a modification of the definition of the taxon, either by intension (diagnosis) or by extension (content) (hence a taxonomic concept). Rule (R8) states that "*once created, any class-series nomen is deemed to preoccupy all possible spellings* derived from the same root [my emphasis], *and applying to taxa of any rank within the class-series*", provided these taxa include the onomatophore (name-bearing type) of the original nomen. Thus, the various spellings that may have been used for a nomen by various authors during the history of taxonomy are just to be considered aponyms of the same nomen, with the same author and date, and not different homonymous nomina with different authors and dates. Among these various spellings, under Rule (R22), the correct one nowadays, or *eunym* (Dubois, 2000), is not necessarily the protonym, but may be one of the aponyms, depending on subsequent usage, as spellings of universal or general usage must be conserved. Many examples of such situations in the class **Amphibia** exist, as shown by a few examples. the aponym **Amphibia** is the eunym of **Amphybiens** De Blainville, 1816; **Batrachia** is that of **Batraciens** Brongniart, 1800 (first latinized as **Batrachii**); **Gymnophiona** that of **Gymnophia** Rafinesque-Schmaltz, 1814; **Anura** that of **Anoures** Duméril, 1806 (first latinized as **Anuri**); **Urodela** that of **Urodeles** Duméril, 1806 (first latinized as **Urodeli**), **Perennibranchia** that of **Perennibranches** Latreille, 1824; etc In all these cases, the author of the protonym remains the author of the nomen even if the eunym is an aponym. Many other examples could be given, in the whole animal kingdom in class-series nomenclature, a large proportion of the nomina currently in use are aponyms ("emendations"), not protonyms (original spellings). It is therefore fully justified to emend such a nomen when it was clearly ill-formed from the start

I propose to take advantage of the possibility offered by these proposed Rules to emend the ill-formed nomen **Terrarana** before it is widely used in the literature. The new spelling should clearly be an aponym of the protonym, i e., it should be derived from the same root, but being a nominative plural and non liable to be confused with a generic nomen based on the nomen *Rana*. The easiest way would be to transfer the original nomen to the nominative plural, as **Terraranae** However, as a change is anyway necessary, one could go even one step further, and take this opportunity to suppress, for reasons of brevity and euphony, the unlucky sound repetition "**rara**" in the original aponym, and to coin the shorter spelling **Terranae** This nomen also includes the two terms used as roots for the protonym, "*terra*" and "*rana*", although more compressed and "overlapping" A similar compression of syllables can be found in other cases, e.g , in the ranid generic nomen *Pulchrana* Dubois, 1992 As analysed in detail in Dubois (1987, 2007*b*) and Dubois & Raffaëlli (2009), the *Code* does not provide Rules or precise guidelines for the construction or for the latinization of nomina, so that such compressed spellings are fully acceptable as some possibilities among several that would derive from the same roots. As for many other class-series nomina, among the two spellings **Terraranae** and **Terranae**, the spelling that will be used by the majority of authors will become the correct one, but the spelling **Terrarana** should not be used

Therefore the new spellings are not new nomina, but aponyms of **Terrarana**, which retains its original authors and date They should be mentioned as "**Terraranae** Hedges, Duellman & Heinicke, 2008" or "**Terranae** Hedges, Duellman & Heinicke, 2008"

UNWARRANTED CREATION OF NOMINA FOR HIGHER TAXA

It should be noted that the two aponyms above are proposed here purely on nomenclatural grounds (explained above) and for nomenclatural purposes. I suggest that, *if* this taxon is to be recognized and given this nomen, *then* the latter should be used under one of these two spellings. This does not mean that I consider warranted either this recognition or, and above all, the fact of affording this taxon a rank above the family-series level. This action was justified by Hedges et al. (2008: 11) mostly on the ground that this group "*is currently considered a single family, (. . .) that is larger than nearly any other family of tetrapods*" and would be made "*more manageable by splitting the group into four families*". According to this strange philosophy, the rank of a taxon would be related to its size (number of included species), which means that it would be based on a quantitative criterion such as Van Valen's (1973) "metataxonomic criterion" (see Dubois, 1988*a-b*). This idea is an old one, but, even with this taxonomic philosophy, it has long been acknowledged that important changes in the ranks of taxa should be done with care: "*What is altogether inadmissible (. . .) is the raising of a single taxon, say, a family, to the rank of order and the concomitant raising of all the subdivisions within this taxon without regard to the consequences for other families in this taxonomic group*" (Mayr & Ashlock, 1991: 273). Hedges et al. (2008) avoided this discussion by failing to consider the consequences of their nomenclatural decision on the other related taxa of anurans.

As recently discussed in detail (Dubois, 2007*a*, 2008*c*), in modern taxonomies which are based on phylogenetic analyses, ranks express cladistic relationships between taxa and sister-group relationships, but they have no other biological or other meaning (Minelli, 2000). This means that taxa sharing the same rank may include widely different numbers of taxa and of subordinate ranks. By itself, such an unbalanced situation is *very informative*. Thus, the existence of a high number of species in the group formerly known as the genus *Eleutherodactylus* Duméril & Bibron, 1841 was telling us something about the rate of speciation in this group, which appears much higher than in other groups of anurans and even of vertebrates, and might be related to their reproductive mode (Dubois, 2004*b*). Splitting this genus into several genera, and its family into several families, obscures this message. It is not at all justified by the fact that these taxa are considered as "clades"[1] as the latter can be recognized at any level in the taxonomic hierarchy, and knowing that a group is holophyletic provides no information on its rank (for more details, see Dubois, 2008*c*).

Hedges et al. (2008) did not discuss the status and nomen of the hypothesized sister-group of their taxon, nor the possibility to still provisionally use higher ranks of the family-series, such as superfamily, epifamily, etc., as suggested by Dubois (2005*c*), in order to avoid the premature creation of class-series nomina. Despite the large amount of new molecular phylogenetic data recently published, the higher taxonomy of the **Amphibia** is certainly still far from being stabilized (see e.g. Wiens, 2007), and it is premature to coin new nomina for higher taxa (all the more that many nomina already exist and can be used for some of these taxa). This problem is particularly strong within the frame of a "pseudo-ranked" nomenclature, such as that used by Frost et al. (2006), which does not provide by itself any information on the hypothesized cladistic relationships between taxa, and especially about sister-group pairs (see Dubois, 2007*a*: 34, 2008*c*). The reality of this problem was clearly

---

[1] Although its has been spreading in the recent literature, the use of the term "clade" to designate taxa is questionable. A clade is a natural lineage in nature, but we never observe (or will observe) clades. We only build hypotheses about clades based on our analyses, and these hypotheses change regularly with new data and analyses. Taxa are *concepts* which, as all scientific concepts and theories, are refutable and abandoned once refuted. It is normal if taxa, which are scientific concepts, change, but "clades", being natural entities, cannot change. We do not need this term in taxonomy. The terms "group", "taxon" or "cladon" (Mayr, 1995) are appropriate to designate the groups suggested by our cladistic analyses.

highlighted by the fact that the same team which proposed many such new class-series taxa (FROST et al., 2006) published a few months later a new work (GRANT et al., 2006) with a new phylogenetic and taxonomic proposal, in which they abandoned one of the new higher nomina introduced just a few months earlier (**DIPHYABATRACHIA**), and introduced several new ones! However, several recent examples show that the community of taxonomists is apparently not prepared to take the time to wait for a stabilized higher taxonomy of the amphibians before proposing well-thought, and also well-formed, short and euphonious nomina for the higher taxa (see DUBOIS & RAFFAËLLI, 2009). Taking this time would indeed certainly have a terrible "psychological" drawback, as it could prevent some taxonomists from "*attaching their names to the new nomina*" (DUBOIS, 2008*a*).

CONSEQUENCES IN CLASS-SERIES NOMENCLATURE

A final note must be added here regarding the Rules for class-series nomenclature proposed by DUBOIS (2006*a*: 227-233). When these Rules were elaborated, I considered it "obvious" that all taxonomists would consider that a class-series nomen should be a noun in the nominative plural, so this was not even mentioned in the proposed Rules. This was a mistake, as nothing is ever "obvious" to all. This severe omission should be corrected in the proposed Rules (R2) and (R3) (DUBOIS, 2006*a*: 227). In Rule (R2), the end of the sentence "*to be available in zoological nomenclature (...), a class-series nomen must have been published (...) as a uninomen*" should be replaced by "*as a uninomen being, or being treated as, a Latin noun in the nominative plural (ending in '-A', '-AE', '-ES', '-I', '-US' or exceptionally '-E')*". The parallel change should be made in Rule (R3), where "*a new class-series nomen should be a Latin or latinized nomen*" should be repaced by "*a Latin or latinized nomen being, or being treated as, a Latin noun in the nominative plural (ending in '-A', '-AE', '-ES', '-I', '-US' or exceptionally '-E')*".

LITERATURE CITED

ANONYMOUS [International Commission on Zoological Nomenclature], 1999. – *International code of zoological nomenclature*. Fourth edition. London, International Trust for zoological Nomenclature: i-xxix + 1-306.

DUBOIS, A., 1984. – La nomenclature supragénerique des Amphibiens Anoures. *Mémoires du Muséum national d'Histoire naturelle*, (A), **131**: 1-64.

---- 1987. – Again on the nomenclature of frogs. *Alytes*, **6** (1-2): 27-55.

---- 1988*a*. – Some comments on the genus concept in zoology. *Monitore zoologico italiano*, (n. s.), **22**: 27-44.

---- 1988*b*. – The genus in zoology: a contribution to the theory of evolutionary systematics. *Mémoires du Muséum national d'Histoire naturelle*, (A), **140**: 1-123.

----- 1992. – Notes sur la classification des Ranidae (Amphibiens, Anoures). *Bulletin mensuel de la Société linnéenne de Lyon*, **61** (10): 305-352.

---- 2000. – Synonymies and related lists in zoology: general proposals, with examples in herpetology. *Dumerilia*, **4** (2): 33-98.

---- 2004*a*. – The higher nomenclature of recent amphibians. *Alytes*, **22**: 1-14.

---- 2004*b*. – Developmental pathway, speciation and supraspecific taxonomy in amphibians. 1. Why are there so many frog species in Sri Lanka? *Alytes*, **22** (1-2): 19-37.

---- 2005*a*. Propositions pour l'incorporation des nomina de taxons de rang supérieur dans le *Code international de nomenclature zoologique*. *In*: A. Dubois, O. Poncy, V. Malécot & N. Léger (ed.), *Comment nommer les taxons de rang supérieur en zoologie et en botanique?*, *Biosystema*, **23**: 73-96.

---- 2005*b*. Proposed Rules for the incorporation of nomina of higher ranked zoological taxa in the *International Code of Zoological Nomenclature*. 1. Some general questions, concepts and terms of biological nomenclature. *Zoosystema*, **27**: 365-426.

---- 2005*c*. *Amphibia Mundi*. 1.1. An ergotaxonomy of recent amphibians. *Alytes*, **23** (1-2): 1-24.

---- 2005*d*. *Amphibia Mundi*. 1.3. Recent amphibians: suprageneric taxonomic additions (1967-2002). *Alytes*, **23** (1-2): 70-80.

---- 2005*e*. Proposals for the incorporation of nomina of higher-ranked taxa into the *Code*. *Bulletin of zoological Nomenclature*, **62**: 200-209.

---- 2006*a*. Proposed Rules for the incorporation of nomina of higher-ranked zoological taxa in the *International Code of Zoological Nomenclature*. 2. The proposed Rules and their rationale. *Zoosystema*, **28**: 165-258.

---- 2006*b*. - Incorporation of nomina of higher-ranked taxa into the *International Code of Zoological Nomenclature*: some basic questions. *Zootaxa*, **1337**: 1-37.

---- 2007*a*. - Phylogeny, taxonomy and nomenclature: the problem of taxonomic categories and of nomenclatural ranks. *Zootaxa*, **1519**: 27-68.

---- 2007*b*. - Genitives of species and subspecies nomina derived from personal names should not be emended. *Zootaxa*, **1550**: 49-68.

---- 2007*c*. Naming taxa from cladograms: some confusions, misleading statements, and necessary clarifications. *Cladistics*, **23**: 390-402.

---- 2007*d*. Nomina zoologica Linnaeana. *In*: Z.-Q. Zhang & W. A. Shear (ed.), *Linnaeus tercentenary: progress in invertebrate taxonomy*, *Zootaxa*, **1668**: 81-106.

---- 2008*a*. A partial but radical solution to the problem of nomenclatural taxonomic inflation and synonymy load. *Biological Journal of the Linnean Society*, **93**: 857-863.

---- 2008*b*. Authors of zoological publications and nomina are signatures, not persons. *Zootaxa*, **1771**: 63-68.

---- 2008*c*. Phylogenetic hypotheses, taxa and nomina in zoology. *Zootaxa*, **1950**: 51-86.

Dubois, A. & Ohler, A., 2008. Nomina Amphibiorum. 1. The status of the amphibian nomina created by Merrem (1820) and Ritgen (1828), with comments on the nomenclatural standards of integrative taxonomy. *Zootaxa*, accepted pending modifications.

Dubois, A. & Raffaëlli, J. 2009. A new ergotaxonomy of the family Salamandridae Goldfuss, 1820 (Amphibia, Urodela). *Alytes*, **26** (1-4): 1-85.

Frost, D. R., Grant, T., Faivovich, J., Bazin, R. H., Haas, A., Haddad, C. F. B., de Sa, R. O., Channing, A., Wilkinson, M., Donnellan, S. C., Raxworthy, C. J., Campbell, J. A., Blotto, B. L., Moler, P., Drewes, R. C., Nussbaum, R. A., Lynch, J. D., Green, D. M. & Wheeler, W. C., 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History*, **297**: 1-370.

Grant, T., Frost, D. R., Caldwell, J. P., Gagliardo, R., Haddad, C. F. B., Kok, P. J. R., Means, D. B., Noonan, B. P., Schargel, W. E. & Wheeler, W. C., 2006. - Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of natural History*, **299**: 1-262.

Hedges, S. B., Duellman, W. E. & Heinicke, M. P. 2008. New World direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation. *Zootaxa*, **1737**: 1-182.

Hillis, D. M., 2006. Constraints in naming parts of the tree of life. *Molecular Phylogenetics & Evolution*, **42**: 331-338.

Kuhn, O., 1967. – *Amphibien und Reptilien*. Stuttgart, Gustav Fischer: i-vii + 1-124.

Linnaeus, C., 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Tomus I. Holmiae, Laurentii Salvii: [i-iv] + 1-824.

Mayr, E., 1995. – Systems of ordering data. *Biology & Philosophy*, **10**: 419-434.

MAYR, E & ASHLOCK, 1991 *Principles of systematic zoology* Second edition New York, McGraw-Hill i-xx + 1 475

MINELLI, A , 2000 – The ranks and the names of species and higher taxa, or a dangerous inertia of the language of natural history. *In* M T GHISELIN & A E LEVITON (ed), *Cultures and institutions of natural history essays in the history and philosophy of sciences*, San Francisco, California Academy of Sciences: 339-351

STAROBOGATOV, Y I , 1991 Problems in the nomenclature of higher taxonomic categories. *Bulletin of zoological Nomenclature*, **48**. 6-18.

VAN VALEN, L., 1973. Are categories in different phyla comparable? *Taxon*, **22**. 333-373

WIENS, J J , 2007. Review of "The amphibian tree of life" *Quarterly Review of Biology*, **82** 55-56

Corresponding editor: Annemarie OHLER

Alytes, 2009, **26** (1-4): 176-180. *Obituary*

Jarujin Nabhitabhata (1950-2008)

Yodchaiy Chuaynkern* ** & Chantip Inthara* ***

* Muséum national d'Histoire naturelle, Departement de Systématique et Évolution,
Reptiles et Amphibiens, CP 30, 25 rue Cuvier, 75005 Paris, France,
<ychuaynkern@yahoo.com>

** Thailand Natural History Museum, National Science Museum, Technopolis,
Khlong 5, Khlong Luang, Pathum Thani 12120, Thailand

*** Department of Biology, Faculty of Science, Khon Kaen University, Muang,
Khon Kaen 40002, Thailand

Jarujin Nabhitabhata (fig. 1), a Thai naturalist, died unexpectedly on 12 September 2008 in Bangkok, Thailand, at the age of 58. For all his friends and colleagues he was "Jarujin", a great lover of natural history and fine expert of wildlife. He was born in Bangkok on 22 January 1950 He graduated from Kasetsart University (Bangkok) with bachelor and master degrees in Science (Agriculture) in 1971 and 1979, respectively The subject of his thesis was the family Tabanidae (Insecta, Diptera).

While studying his Master degree, Jarujin made an important experience working with a great Thai naturalist, Dr Boonsong Lekagul (1907-1992). Jarujin also worked at the Association for the Conservation of Wildlife to collect butterflies in many parts of the country. In 1966, he started his work at the Centre for the Thai National Reference Collection of the Thailand Institute of Scientific and Technological Research (TISTR) Staying over 31 years in this institute, he spent most of his time collecting animal specimens throughout the country When the Thailand Natural History Museum (THNHM) was successfully established in 1977, Jarujin moved to work there and many scientific specimens from the TISTR were transferred to its collection. He worked at this place until his last day, ending his career as the Director of the Thailand Natural History Museum.

The establishment of the natural history museum in Thailand was instigated by Jarujin's master Boonsong This effort begun by collaboration with both foreigners and Thais for exploring the fauna and collecting scientific specimens (e g , amphibians, reptiles, birds, mammals) throughout the country. The results of these faunal biodiversity explorations were presented in various forms, especially books *Field guide to the butterflies of Thailand* (Lekagul et al , 1977), *Mammals of Thailand* (Lekagul & McNeely, 1998), *A field guide to the birds of Thailand* (Lekagul & Round, 1991) These books were related in various ways with Jarujin's activity, as co-author, collector of specimens, or author of suggested Thai names for many species. Unfortunately, the establishment of the natural history museum did not happen in the life time of Boonsong but it was accomplished during Jarujin's life.

Fig 1 Jarujin Nabhitabhata (1950-2008) in 2007 Photograph courtesy of Smithi Satabutr

Until the last day of his life, Jarujin kindly collaborated with both foreign and domestic scientists in elucidating the faunal diversity of Thailand. Regular faunal summaries and updates in the form of books (e.g , NABHITABHATA, 1988; COX et al., 1998; NABHITABHATA & SUWANNAPHAK, 2001; SUWANNAPHAK & NABHITABHATA, 2008) and checklists (e.g NABHITABHATA et al , 2004; NABHITABHATA & CHAN-ARD, 2005) were published as the sum of observations accumulated over the years. Along with his entomologist colleagues, he described the beetle *Aesalus dharma* (Coleoptera, Lucanidae) (ARAYA et al , 1994). In the field of batrachology, four new species of anurans were described from Thailand: *Ansonia inthanon* (MATSUI et al , 1998), *Leptobrachium smithi* (MATSUI et al , 1999), *Ansonia kraensis* (MATSUI et al., 2005) and *Amolops panhai* (MATSUI & NABHITABHATA, 2006). As for reptiles, seven new species of lizards were described: *Gekko taylori* (OTA & NABHITABHATA, 1991), *Dibamus somsaki* (HONDA et al., 1997), *Ptyctolaemus phuwuaensis* (MANTHEY & NABHITABHATA, 1991), *Tropidophorus latiscutatus* (HIKIDA et al , 2002), *Tropidophorus matsui* (HIKIDA et al., 2002), *Tropidophorus murphyi* (HIKIDA et al , 2002) and *Tropidophorus hangnam* (CHUAYNKERN et al., 2005) In recognition for his efforts, at least six new species of animals were named after him for his contribution to the study of natural history in Thailand. *Liphistius jarujini* (Arachnida, Liphistiidae) (ONO, 1988), *Potamon jarujini* (Decapoda, Potamidae) (NG & NAIYANETR, 1993), *Cyrtodactylus jarujini* (Squamata, Gekkonidae) (ULBER, 1993), *Coniocompsa nabhitabhata* (Neuroptera, Coniopterydidae) (SZIRÁKI, 2002), *Platyroptilon jarujini* (Diptera, Keratoplatidae) (PAPP et al , 2006), *Rhacophorus jarujini* (Amphibia, Rhacophoridae) (Matsui & Panha, 2006) and *Trichogalumna nabhitabhatai* (Acari, Galumnidae) (Mahunka, 2008).

Jarujin also worked as invited professor for several universities: Chulalongkorn University (Bangkok), Kasetsart University (Bangkok), Mahidol University (Bangkok), Mahasarakham University (Bangkok). Along with various professors of these universities, he laid the basic framework for biological studies for students. The results of this effort is reflected in the numerous thesis defended by his students (e.g., Chan-ard, 1987; Jeerasuksaliew, 1991; Phluengchien, 1994; Inthara, 2000; Chuaynkern, 2001; Noikotr, 2001; Sukprakarn, 2003; Taksintum, 2003; Meewattana, 2005) and the research articles published in common (e.g., Sukprakarn & Nabhitabhata, 2003, Kongcharoen & Nabhitabhata, 2007; Inthara et al., 2005). His students are now working in several government agencies, NGOs or companies and now strongly participate in efforts concerning conservation policy and biological study in Thailand. To acknowledge his effort as a teacher, Jarujin was offered in 2004 the honorary doctorate degree in Biology from Mahasarakham University. This was the final recognition of the scientific importance of a life dedicated to exploration of wildlife in abundant collaboration.

Beside from his friends, colleagues or students, Jarujin Nabhitabhata should receive broad respect for his devotion to his career. Everyone's life has a last day, and Jarujin has attained it before us. For all of us his early and unexpected disappearance happened at the inappropriate moment. His name and his contributions on natural history will be reminded forever.

ACKNOWLEDGEMENTS

We thank Worrawarai Seleewong (THNHM) for providing and confirming some information. Annemarie Ohler and Alain Dubois are thanked for their kindness of correcting and editing our draft. We also thank Wachara Sanguansombat (THNHM) for providing Jarujin's photograph.

LITERATURE CITED

Araya, K., Matsui, M., Nabhitabhata, J. & Panha, S., 1994. A new Bristly *Aesalus* (Coleoptera, Lucanidae) from Peninsular Thailand. *Giorn. ital. Entom.*, 7: 73-77.

Chan-ard, T., 1987. *Species diversity of amphibians in Huai Khakhaeng Wildlife Sanctuary, Uthai Thani and Tak Provinces*. Ms Thesis, Bangkok, Kasetsart University [In Thai with English abstract].

Chuaynkern, Y., 2001. *Species diversity of amphibians and reptiles at Pang Sida National Park, Sakaeo Province*. Ms Thesis, Bangkok, Kasetsart University [In Thai with English abstract].

Chuaynkern, Y., Nabhitabhata, J., Inthara, C., Kamsook, M. & Somsri, K., 2005. A new species of the Water skink *Tropidophorus* (Reptilia, Squamata, Scincidae) from Northeast Thailand. *Thailand nat. Hist. Mus. J.*, 1: 165-175.

Cox, M. J., Van Dijk, P. P., Nabhitabhata, J. & Thirakhupt, K., 1998. *A photographic guide to snakes and other reptiles of Thailand and Southeast Asia*. Bangkok, Asia Books: 1-144.

Hikida, T., Orlov, N. L., Nabhitabhata, J. & Ota, H., 2002. Three new depressed-bodied water skinks of the genus *Tropidophorus* (Lacertilia, Scincidae) from Thailand and Vietnam. *Curr. Herp.*, **21**: 9-23.

Honda, M., Nabhitabhata, J., Ota, H. & Hikida, T. 1997. – A new species of *Dibamus* (Squamata: Dibamidae) from Thailand. *Raffles Bull. Zool.*, **45**: 276-279.

Inthara, C., 2000. – *Study on mouthparts structures in relation to feeding behavior of some tadpole species.* Ms Thesis, Bangkok, Kasetsart University. [In Thai with English abstract].

Inthara, C., Laohachinda, V., Nabhitabhata, J., Chuaynkern, Y. & Kumtong, P., 2004. – Mouth part structures and distribution of some tadpoles from Thailand. *Thailand nat. Hist. Mus. J.*, **1**: 55-78.

Jeerasuksaliew, S., 1991. – *Species diversity of amphibians and reptiles in different utilization area in Rayong Province*. Ms Thesis, Kasetsart University, Bangkok. [In Thai with English abstract].

Kongcharoen, W. & Nabhitabhata, J., 2007. – Species diversity and altitudinal distribution of the amphibians along Lam Ta Klong stream area in Khao Yai National Park. *J. Wildl. Thailand*. **14**: 113-128.

Lekagul, B., Askins, K., Nabhitabhata, J. & Samruadkit, A., 1977. – *Field guide to the butterflies of Thailand*. Bangkok, Association for the Conservation of Wildlife: 1-260.

Lekagul, B., & McNeely, J. A., 1988. – *The mammals of Thailand*. Bangkok, Saha Karn Bhaet Co.: 1-758.

Lekagul, B., & Round, P. D., 1991. – *A guide to the birds of Thailand*. Bangkok, Saha Karn Bhaet Co.: 1-457.

Mahunka, S., 2008. – A new genus and some other data of oribatids from Thailand (Acari: Oribatida). *Acta zoologica Academiae Scientiarum hungaricae*, **54**: 125-150.

Manthey, U., & Nabhitabhata, J., 1991. – Eine neue Agame, *Ptyctolaemus phuwuaensis* sp.n. (Sauria: Agamidae), aus Nordost-Thailand. *Sauria*, **13**: 3-6.

Matsui, M., Khonsue, W. & Nabhitabhata, J., 2005. – A new *Ansonia* from Isthmus of Kra, Thailand (Amphibia, Anura, Bufonidae). *Zool. Sci.*, **22**: 809-814.

Matsui, M. & Nabhitabhata, J., 2006. – A new species of *Amolops* from Thailand (Amphibia, Anura, Ranidae). *Zool. Sci.*, **23**: 727-732.

Matsui, M., Nabhitabhata, J. & Panha, S., 1998. – A new *Ansonia* from northern Thailand (Anura: Bufonidae). *Herpetologica*, **54**: 448-454.

---- 1999. – On *Leptobrachium* from Thailand with a description of a new species (Anura: Pelobatidae). *Jap. J. Herp.*, **18** : 19-29.

Matsui, M. & Panha, S., 2006. – A new species of *Rhacophorus* from eastern Thailand (Anura: Rhacophoridae). *Zool. Sci.*, **23**: 477-481.

Meewattana, P., 2005. – *Morphological characters for identification of anuran tadpoles in Khao Luang National Park, Khlong Nakha and Hala-Bala Widlife Sanctuary.* PhD Thesis, Bangkok, Kasertsart University.

Nabhitabhata, J., 1988. – *Amphibians*. Bangkok, Business Organization of the Teachers' Council of Thailand: 1-56. [In Thai].

Nabhitabhata, J. & Chan-ard, T., 2005. – *Thai red data: mammals, reptiles and amphibians*. Bangkok, Office of Natural Resources and Environmental Policy and Planning: 1-234.

Nabhitabhata, J., Chan-ard, T. & Chuaynkern, Y., 2004. – *Checklist of amphibians and reptiles in Thailand*. Bangkok, Office of Environmental Policy and Planning, "2000": 1-152.

Nabhitabhata, J. & Suwannaphak, K., 2001. – *Field guide of the butterflies in Thailand.* Bangkok, Wana Press: 1-320. [In Thai].

Ng, P. K. L. & Naiyanetre, P., 1993. – New and recently described freshwater crabs (Crustacea: Decapoda: Brachyura: Potamidae, Gecarcinucidae and Parathelphusidae) from Thailand. *Zoologische Verhandelingen*, **284**: 1-117.

Noikotr, K., 2001. – *Diversity of mature anurans and their tadpole in Khao Kitchakut National Park area, Chanthaburi Province.* Ms Thesis, Bangkok, Kasetsart University. [In Thai with English abstract].

Papp, L., Merz, B. & Földvári, M., 2006. – Diptera of Thailand: a summary of the families and genera with references to the species representations. *Acta zoologica Academiae Scientiarum hungaricae*, **52**: 97-269.

Philuengchien, V., 1994. – *A species survey of amphibians in Khao Khiew-Khao Chomphu, Chon Buri Province*. Ms Thesis, Bangkok, Kasetsart University. [In Thai with English abstract].

Ono, H., 1998. – Liphistiid spiders (Araneae, Mesothelae) of northwest Thailand. *Bull. natn. Sci. Sci. Mus.*, Tokyo, **14**: 35-41.

OTA, H. & NABHITABHATA, J., 1991. – A new species of *Gekko* (Gekkonidae: Squamata) from Thailand. *Copeia*, **1991**: 503-509.

SUKPRAKARN, N., 2003. – *Species diversity and habitats of amphibians and reptiles at Namtok Phliu National Park, Chanthaburi Province.* Ms Thesis, Bangkok, Kasetsart University. [In Thai with English abstract].

SUKPRAKARN, N. & NABHITABHATA, J., 2003. – Species diversity and habitats of amphibians and reptiles at Namtok Phliu National Park, Chanthaburi Province. *In*: V. BAIMAI & R. TANTALAKHA (ed.), *BRT Research Report 2003*, Bangkok, Chuan Printing Press Ltd.: 235-244. [In Thai with English abstract].

SUWANNAPHAK, K. & NABHITABHATA, J., 2008. – *Field guide of insects.* Bangkok, Sarakadee Press: 1-224. [In Thai].

SZIRÁKI, G., 2002. – Coniopterygidae (Neuroptera) from Thailand. *Folia ent. hungarica*, **63**: 53-64.

TAKSINTUM, W., 2003. – *Diversity of mature frogs and their tadpole in Khlong Sang Wildlife Sanctuary.* Ms Thesis, Bangkok, Kasetsart University. [In Thai with English abstract].

ULBER, T., 1993. – Bemerkungen über cyrtodactyline Geckos aus Thailand nebst Beschreibungen von zwei neuen Arten (Reptilia: Gekkonidae). *Mitt. zool. Mus. Berlin*, **69**: 187-200.

ALYTES

International Journal of Batrachology

published by ISSCA

SHORT GUIDE FOR AUTHORS

(for more detailed *Instructions to Authors*, see *Alytes*, 1997, **14**: 175-200)

Alytes publishes original papers in English, French or Spanish, in any discipline dealing with amphibians. Beside articles and notes reporting results of original research, consideration is given for publication to synthetic review articles, book reviews, comments and replies, and to papers based upon original high quality illustrations (such as colour or black and white photographs), showing beautiful or rare species, interesting behaviours, etc.

The title should be followed by the name(s) and address(es) of the author(s). The text should be typewritten or printed double-spaced on one side of the paper. The manuscript should be organized as follows: English abstract, introduction, material and methods, results, discussion, conclusion, French or Spanish abstract, acknowledgements, literature cited, appendix.

Figures and tables should be mentioned in the text as follows: fig. 4 or tab. 4. Figures should not exceed 16 × 24 cm. The size of the lettering should ensure its legibility after reduction. The legends of figures and tables should be assembled on a separate sheet. Each figure should be numbered using a pencil.

References in the text are to be written in capital letters (BOURRET, 1942; GRAF & POLLS PELAZ, 1989; INGER et al., 1974). References in the *Literature Cited* section should be presented as follows:

BOURRET, R., 1942. – *Les batraciens de l'Indochine*. Hanoi, Institut Océanographique de l'Indochine: i-x + 1-547, pl. 1-4.

GRAF, J.-D. & POLLS PELAZ, M., 1989. – Evolutionary genetics of the *Rana esculenta* complex. *In*: R. M. DAWLEY & J. P. BOGART (ed.), *Evolution and ecology of unisexual vertebrates*, Albany, The New York State Museum: 289-302.

INGER, R. F., VORIS, H. K. & VORIS, H. H., 1974. – Genetic variation and population ecology of some Southeast Asian frogs of the genera *Bufo* and *Rana*. *Biochem. Genet.*, **12**: 121-145.

Manuscripts should be submitted either as attached document by e-mail, or in paper form by mail but then **in triplicate**, either to Alain DUBOIS (address above) if dealing with amphibian morphology, anatomy, systematics, biogeography, evolution, genetics, genetics, anomalies or developmental biology, or to Franco ANDREONE (address above) if dealing with amphibian population genetics, ecology, ethology, life history or conservation biology, including declining amphibian populations or pathology. Acceptance for publication will be decided by the editors following review by at least two referees.

After acceptance, a copy of the final manuscript should be sent to the Chief Editor, either as attachment by e-mail, or by mail on a floppy disk (3 ½ or 5 ¼). We welcome the following formats of text processing: (1) preferably, MS Word (1.1 to 6.0, DOS or Windows), WordPerfect (4.1 to 5.1, DOS or Windows) or WordStar (3.3 to 7.0); (2) less preferably, formated DOS (ASCII) or DOS-formated MS Word for the Macintosh (on a 3 ½ high density 1.44 Mo floppy disk only).

Page charges are requested only from authors having institutional support for this purpose. The publication of colour photographs is charged. For each published paper, a free pdf or 25 free reprints are offered by ISSCA to the author(s). Additional reprints may be purchased.

Published with the support of AALRAM
(Association des Amis du Laboratoire des Reptiles et Amphibiens
du Muséum National d'Histoire Naturelle, Paris, France).
Directeur de la Publication: Alain DUBOIS.
Numéro de Commission Paritaire: 64851.

Alytes, 2009, **26** (1-4): 1-180.

Contents

Alain Dubois & Jean Raffaëlli
A new ergotaxonomy of the family Salamandridae Goldfuss, 1820 (Amphibia, Urodela) 1-85

Chantip Inthara, Yodchaiy Chuaynkern, Prateep Duengkae & Stéphane Grosjean
The tadpole of *Quasipaa fasciculispina* (Inger, 1970) from southeastern Thailand, with the description of its buccal anatomy 86-96

S. Hareesh Joshy, Mohammad Shafiqul Alam, Atsushi Kurabayashi, Masayuki Sumida & Mitsuru Kuramoto
Two new species of the genus *Euphlyctis* (Anura, Ranidae) from southwestern India, revealed by molecular and morphological comparisons 97-116

Marjolein Kamermans & Miguel Vences
Terminal phalanges in ranoid frogs: morphological diversity and evolutionary correlation with climbing habits 117-152

Roger Bour, Annemarie Ohler & Alain Dubois
The onomatophores of *Paramesotriton deloustali* (Bourret, 1934)........ 153-166

Alain Dubois
Miscellanea nomenclatorica batrachologica.
20. Class-series nomina are nouns in the nominative plural: Terrarana Hedges, Duellman & Heinicke, 2008 must be emended 167-175

OBITUARY

Yodchaiy Chuaynkern & Chantip Inthara
Jarujin Nabhitabhata (1950-2008) 176-180

Alytes is printed on acid-free paper.

Alytes is indexed in *Biosis*, *Cambridge Scientific Abstracts*, *Current Awareness in Biological Sciences*, *Pascal*, *Referativny Zhurnal* and *The Zoological Record*.

Imprimerie F. Paillart, Abbeville, France.
Dépôt légal: 1er trimestre 2009.